A CRITICAL REVIEW OF PRESENT DAY KNOWLEDGE OF THE NATURE OF HUNGER.

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PREFACE.

There can be no doubt that hunger is one of the most fundamentally important experiences in the life of every organism, and that it is a factor which has played a dominant part in the history of Man, and indeed of all animals, cannot be denied.

No subject could be more profitably surveyed since its influence involves such vital issues.

Despite the fact that hunger is so universal a problem one must admit that, compared with other questions arising in connection with our existence, the matter has received comparatively scanty attention. This state of affairs is due possibly to the fact that hunger, as a sensation, is hard to analyse since its disagreeable effect on consciousness induces other conflicting elements of an emotional nature so that a logical study of the already complex process is rendered more difficult. If hunger, regarded in its wider sense, does occur in animals it is probable that in them, lacking as they do the higher cerebral centres, the sensation is less complicated than in man, but, for obvious reasons, the study of the problem in them must be limited largely to objective phenomena secondary to hunger.

References to the literature in relation to hunger will be given in the appendix, and it has been thought advisable to classify the authors alphabetically in preference to the more complicated numerical method of quoting the source of the information.

A CRITICAL REVIEW OF PRESENT DAY KNOWLEDGE OF THE NATURE OF HUNGER.

Chapter I.

I N T R O D U C T I O N

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Hunger is an inherent urge for the nourishment of the individual, in the same way that the sexual instinct is designed for the preservation of the race.
The problem of hunger appears to be intimately bound up with the life of all animal organisms.
Considered biologically, this sensation-complex appears, indeed, to be more fundamental than the sexual urge, in view of the fact that the taking of nourishment is essential to living organisms whereas sexual reproduction is not.
The Hunger sensation, as one ascends in the animal scale, involves a correspondingly greater complexity of processes especially with regard to the Central Nervous System, and as a sensation, (and therefore a conscious process) it probably occurs only in organisms possessing a nervous system and an alimentary tract. In view of the fact that all living organisms feed, it is evident that in them there must be some mechanism, no matter how primitive, which enables them to track down and ingest various products. Thus, there appears to be the same essential principle involved in the amoeba which feeds on the protozoan and the wolf which hunts and devours its prey.
The mode of feeding in the simpler parasitic organisms is essentially that of the tissue cells of the mammals, in that nourishment is in solution in the medium in which the cell finds itself.
In organisms consisting of a single cell, feeding appears to be more or less automatic and particles are taken up irrespective of their nutrient value, the degree with which this process takes place appearing to be determined by the activity of the organisms. An increase in the motility is, apparently, the only evidence we possess, so far, that amoebae, for instance, are in a state of hunger although the quiescent state does not necessarily appear to be associated with the digestion of the engulfed food particles. As far as we know, motility in protozoa is automatic and ceases only when the organism is moribound from lack of nourishment.
In Sea-anemon es there is some evidence of specialization with regard to feeding, as shown by the fact that meat extract in the water produces a current directing the nutrient substances into the gullet by means of the labial cilia. (Parker).

As regards food elements in solution the process of ingestion has been thought to depend on the same laws of diffusion and permeability of cell-membranes, such as obtains in all types of organisms and tissue-cells.
Regarding the state of hunger in protozoa, it is likely that the ingestion of soluble food is effected by diffusion and selective absorption, whilst that of solids involves an inherited mechanism whereby the response to chemical and mechanical stimuli is determined.

Hunger sensation in Man is associated with a feeling of discomfort or tension (varying from pressure to pain) localised to the epigastrium, whilst there may be a sense of 'emptiness' in the same situation. Cannon and Washburn and others have pointed out that periodicity is a characteristic feature of the stomach (empty or otherwise), whilst there may be a not unpleasant sensation, at the same time, referable to the gullet, throat, and muscles of mastication.
The essential factor in hunger is the epigastric sensation (Carlson) but various adventitious symptoms and signs may become evident, such as weakness, headache, nausea, nervous irritability etc.; but whilst the last-named has been shown to be a necessary result of hunger, in any degree, the other phenomena should not occur normally, but in neurotic patients they may assume such prominence as to mask the main factor, namely the gastric hunger-pangs.
Normally, in man, hunger is a rare experience since it requires an empty or nearly empty stomach to produce the hunger-sensation., and so, owing to the fact that three or four meals are taken daily, this state seldom occurs.
It is generally held that, except in those subjected to great physical exertion or intense cold, nervous impulses from the stomach, as a result of hunger contractions, are inadequate to affect consciousness. The origin of hunger is, according to Carlson and his School, due to the effect on certain areas of the brain of afferent nervous impulses due to gastric motility consequent upon lack of food, and thus it is evident that the mechanism of hunger involves a Central Nervous System, afferent nerves and a muscular alimentary tract. The nervous excitability resulting from a state of hunger, occuring as it does in decerebrate animals, is presumably independent of the appreciation in consciousness of the hunger sensation.
Extreme hunger in animals may lead to the loss of fear and the exhibition of savage traits, whilst in man it produces, or tends to produce, nervous irritability. The effect of the hunger state differs in various individuals, for, whilst in the man who has perforce to go hungry it may produce a cantakerous disposition, in the man who starves on religious grounds it produces an elevating mental effect. In the latter instance it is evident that a person who can resist two fundamental instincts, viz.- by remaining celibate and enduring hunger-pangs, has a remarkable degree of will-power. It is clear, therefore, that the degree of

discomfort produced by hunger depends largely upon the mentality of the individual concerned.
Whilst in carnivora (including man) an empty, or nearly empty, stomach is required to produce a feeling of hunger, this is not so in ruminants or herbivora since in them the stomach is never empty, and furthermore, birds, even in the presence of a full crop or stomach, are known to feed more or less continuously.
Presumably these animals experience hunger apart from the condition of the stomach or else the factor which leads to feeding is not the hunger-urge but appetite.
Certain circumstances appear to point to the fact that at times the hunger sensation is in abeyance in some organisms, e.g. a species of salmon discontinues feeding when spawning although during that season it would seem that nourishment would be particularly indicated; again, animals in captivity may resist efforts to feed them and may starve in the presence of plenty of food; the caterpillar has been described by Haller (the physiologist) as "doing nothing but eating and defaecating" although after changing into a butterfly it may never feed again. The urge of hunger, when sufficiently strong, will waken the sleeping animal but not the hibernating animal.
Despite these apparent discrepancies, the view that it is the hunger-urge which normally leads to feeding and that the empty stomach plays a part in the origin of this urge remains unaffected, and the above paradoxes must be attributed to fundamental changes in the function of the normally acting hunger mechanism characteristic of the particular organism involved at certain stages of its existence. Apart from these seeming exceptions, a general statement may be made to the effect that normally the degree of the hunger-urge is closely correlated to the metabolic rate and activity of the organism.
That hunger is intimately bound up with metabolism is suggested by the fact that it is more marked in youth than in old age and is intensified by external cold and exercise (both factors which increase tissue functions). Exophthalmic goitre, producing, as it does, an increased metabolic rate, is associated in its early stages with the augmentation of hunger.
The knowledge that eating abolishes the hunger sensation is the experience of all animals but, since in the newly-born creature such knowledge does not exist, taking food for the first time must owe its origin to instinct or inherited reflexes.
Thus various authors may justly consider that hunger is not primarily a sensation but an instinct. In addition to possessing a feeding reflex the new born animal also possesses defensive reflexes enabling it, amongst other things, to reject nocuous substances in the mouth. Gastric motility, on this assumption, merely increases the reflex excitability so that the feeding reflex is rendered more active, and locomotion, if possible, is induced.

The feeding reflex per se appears to be independent of the cerebral cortex as in decerebrated pigeons restlessness and locomotion is increased when the crop is empty so that whilst the bird picks at food - in other words, exhibits movements associated with the act of feeding - it fails to recognise it as food. This proves that the state of hunger induces motility directed towards nourishment but the absence of the cortex causes the bird to fail to exhibit judgment, will or desire in respect of food - which ultimately determines the actual ingestion of food substances.

It is interesting to note that in the newly born animal objects are directed towards the mouth indiscriminately, but their final adoption or rejection is determined by the feeding or the defensive reflex called into action by the physical or chemical nature of the substance. Certain acts in the new-born in connection with feeding such as sucking and swallowing are instinctive but the ultimate relation between the hunger-urge and feeding processes has to be appreciated by the individual as the result of experience.

Pavlov has postulated a reflex of purpose. He defines "inborn basic nervous activity presenting itself as a group of reactions of the organism to definite external or internal stimuli", each reaction being an instinct or reflex. According to him, all life is but the realisation of one purpose, namely its preservation. The feeding reflex amongst a large number of other reflexes enables this state to be accomplished. Further, he emphasises that periodicity is vital in the reflex of purpose and maintains that if periodicity is not conformed to in feeding the young animal will eventually exhibit a weakening of the food reflex. It is a common-place observation that the eating of sweets between meals destroys the capacity of the child to eat normal amounts of food. Another significant fact is that if purpose goes, life ceases to be attractive; instances of this occur in the practice of the physician where patients who fail to find a purpose in life exhibit a disinclination for food which may ultimately lead to the death of the individual from starvation.

The link between the individual and his surroundings is largely that of food, and external stimuli act as the signals. In the more primitive organism the assimilation of food is determined by the direct contact of the cell with the nutrient substance, but in the more complex higher animals the agents which lead to the assimilation of food are odours, sight, sounds etc. This results in the development of a movement reaction of the organism towards food. Thus it is that the smell or sight of food is the conditioned reflex which determines the complex nervous control of the salivary and gastric glands. Pavlov does not, in actual words, describe hunger and appetite as being separate entities, as other authorities do, but appears to regard both as part of the reaction on the part of the organism

towards nourishment via the food centre.
Carlson emphasises the importance in feeding of augmentation of all reflexes by the gastric hunger state, removal of hunger pangs, and the production of a state of satiety in the infant, by sucking and the ingestion of food; memory is an additional necessity since otherwise every feeding would involve trial and error.
The question of whether hunger, in its purely subjective sense, and the ingestion of food in the new born are linked by means of the factor of appetite is uncertain. In fact it has not been definitely and finally proved whether hunger and appetite are fundamentally different, or only different degrees of the same process, although as will be shown later the former theory is generally considered the more likely.
It is important to note that appetite cannot be considered apart from the memory of past experience with food and, indeed, as Hoelzel points out, it appears to depend upon a taste-memory complex. Furthermore, the memory processes in relation to feeding in the past are pleasant so that the desire to repeat the pleasure may account for the development of appetite.
On the other hand, appetite may involve an elemental inherited urge-factor for food independent of individual experience, although in the adult this experience may combine with or outweigh the importance of the inherited factor. If we assume that such an inherited appetite urge does exist, this, plus the instinctive carrying of all substances to the mouth seen in the new born, may account for the taking of food even in the absence of hunger, but if hunger is present the relief of the unpleasant hunger pangs by taking food is completed by the experience.
It is clear, therefore, that the initiation of feeding in the newly born child may occur in one of two ways (Carlson) :-

1. In the presence of hunger pangs, increased motility, and reflex excitability, plus the inherited reflex of placing all within reach into the mouth, plus the defensive reflexes (for the discarding of nocuous substances), all that is required is that the food should be within reach for ingestion to occur. The experience of the relief of unpleasant hunger pangs by food ingestion is then rapidly evolved.
2. Assuming an inherited appetite urge (positive chemotropism) so that certain olfactory and gustatory stimuli initiate and direct the reflexes towards food, ingestion is just as likely to occur as in the first instance.

The experience of feeding once having been established the process is repeated because of the pleasure associated with food and satiety, or because food relieves the unpleasant hunger pangs.
Katz has advanced a Two-Component Theory of Hunger in which he shows that the condition depends upon:- (a) The psycho-physiological condition of the subject (b) certain

external factors related to the food, feeding, or the individual concerned.
This will be dealt with in a later chapter.
It should be noted that where "food" has so far been referred to, this term includes all substances essential to life in the animal under discussion, viz. organic (including vitamines) and inorganic materials.
Although natural food contains salts of various kinds necessary to support life, in certain instances these have to be added to, especially in the diet of herbivora, in order to prevent distress arising from inadequate amounts of such salts. It apparently happens that should sodium chloride be deficient in the diet of an animal the latter experiences an urge for salt ("salt-hunger") and takes steps to correct this defect by seeking for itself for such substances; a defect in NaCl content of food is thought to lead in time to lack of HCl in the gastric juice and finally anorexia may supervene in consequence. The means whereby animals are able to remedy a salt defect seems to involve the same problem as that of the relief of hunger by feeding.
As regards other substances necessary to support life, for example water and air, the question of regulating the supply of the former depends upon thirst (a subjective sensation indicating de-hydration of the tissues generally), whilst a lack of the latter shows itself by dyspnoea (resulting from a varying degree of anoxaemia). The biological necessity for water and air is independent of the factor of appetite although it is clear that in the case of fluid nourishment an appetite may be developed for the contained substances, apart from thirst, e.g. beer and tea.
It is striking to note that the more fundamental the biological essentials are, the less is the need for the augmentation of their attractiveness by the complex factor of appetite, which, after all, is a refinement associated with ingestion of food in the higher animals only; thus for the amoeba a substance is either nutritive or nocuous whilst in the more complex organism nutritive substances are subject to a further scrutiny depending largely upon the past experience of the animal with food principles.
To summarise what has been said, facts suggest that hunger is a biological primeval urge for food designed for the maintenance of life in the individual and that in the higher animals the hunger sensation develops possibly in response to the stimulation of specialised parts of the central nervous system by the periodic motility of empty viscera, in association with lack of nutriment in the body tissues or blood.
Nutrition is thus as fundamental as respiration, both of which mechanisms exhibit periodic activity of their own with nervous connections modifying their functions.

Hunger precedes the appearance of the muscular alimentary tract, as indications of its presence are seen in very primitive forms of life, but the hunger sensation in man appears to be associated with certain manifestations of activity in the empty stomach and bowel and changes in the central nervous system resulting from, or occurring in conjunction with, these visceral manifestations. In other words, hunger may be regarded as a general sensation with a local reference and without any special region of origin or it may be considered as having a local source and a local reference.

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Chapter II.

HUNGER AND APPETITE.

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Before entering into the question of the mechanism of hunger, the role of the stomach in its relation to hunger sensation, and other factors causing changes (peripherally or centrally) in connection with the above sensation, as well as a consideration of the position now held regarding the hunger state, it is necessary to distinguish between hunger and appetite and to present certain views which help to clear up any ambiguity which may exist concerning each factor.
As we have seen in the introduction, caterpillars eat continuously and apparently in excess of their physiological needs, which seems to indicate that feeding for them is more or less the sole purpose of existence. In man and higher animals feeding is periodic since the sequence is as follows:- Hunger leads to eating and is relieved by food, which, if taken in sufficient amounts, produces satiety; food eaten in excess of this induces unpleasant epigastric fullness and nausea so that feeding is discontinued and when, after digestion, the stomach becomes empty, or nearly so, the hunger sensation arises again and food ingestion is again resorted to. It hardly seems necessary to point out that normally we need not fill our stomachs to the point of distention in order to be certain of ingesting satisfactory amounts of nourishment for ordinary purposes, but it is our experience that if food is rendered extremely palatable we are inclined to eat far in excess of what is required for our body-needs. In other words, the amount of food necessary to relieve the hunger sensation and to suffice for metabolic needs is greatly exceeded because attractive food induces marked appetite, which is essentially pleasant, as opposed to hunger, which is usually unpleasant and occasionally painful. This is an important point since upon it rests the clue to avoiding dietetic excesses, viz: the substitution of plain fare, which is adequate for body needs, for the highly flavoured luxurious meals of modern civilisation, which by whetting the appetite leads to blinding of the dietetic judgment.
Carlson has obtained successive contrasts of hunger and appetite experimentally by means of introducing wine into the empty stomach via the stomach tube (the latter was employed in order to avoid the production of gastric secretion by stimulation of the mouth and gullet by the wine). He found objectively that the gastric hunger contractions, which he considers give rise to the hunger

sensation, were temporarily inhibited (presumably by stimulation of the gastric mucosa) whilst the unpleasant pangs associated with hunger were replaced by pleasant sensations related to food ingestion and typical of appetite. The fact that taking food stimulates the appetite and abolishes hunger, for shorter or longer periods, is illustrated by the saying "L'appetit vient en mangeant" and tends to show not only that hunger and appetite are qualitatively different but, in this respect, seem to be in some degree antagonistic sensations or contrasting functions.

Thus, whereas hunger produces crude unpleasant sensations associated with the necessity for food, appetite produces finely discriminating sensations associated with the act of feeding and the relief of hunger pangs.

Boring, although he disagrees with Carlson's findings in experimentally producing alternation of hunger and appetite, agrees that a meal taken during the hunger state enables appetite to be distinguished from hunger. He maintains too, that whereas hunger is a complex of kinaesthetic pressure and pain referred to the stomach, in appetite, on the other hand, gastric sensations are sometimes absent or not very evident; mouth and gullet sensations are experienced in appetite, however.

Pavlov regards hunger as an inborn reflex whilst appetite is virtually a conditioned (conditional) reflex and this conception is supported by the fact that hunger is dependent almost exclusively upon internal stimuli - appetite however is largely concerned with external stimuli.

Weber expresses hunger as being essentially katabolic - its existence is designed to urge the search for nourishment. Food having been obtained, appetite arises an an anabolic factor related to digestive and anabolic processes. This author also, in considering the psychological aspects of hunger and appetite, correlates the two divergent physiological states by indicating that, taking everything into consideration, hunger appears to concern the unconscious mind whilst appetite is related to the conscious mind. Hunger, being a manifestation of a primitive instinctive activity and arising in order to preserve the individual, may be compared to the reaction of the organism to nocuous stimuli when pain is produced - namely, by suddenly thrusting itself into consciousness, submerging everything in the conscious field, and demanding instant satisfaction. This explains why individuals, who still possess the desire to live, commit the crime of stealing food irrespective of consequences in order to appease the urgent hunger pangs. The consumption of this food is surely unassociated with appetite if hunger is so overwhelmingly powerful, or, as a typically pleasurable sensation, it may for all practical purposes be disregarded.

Carlson points out that given a certain complex from the viscera and approximately normal central correlations - all that is necessary for the existence of hunger - the

central and essential element in appetite is the memory of past experiences (smell, sight, taste) of palatable foods; such memories may naturally be reinforced by external factors e.g. the act of eating itself.
Muller regards hunger as being a motor rather than a sensory phenomenon and compares it to the impulse to breathe, but it is obviously less urgent than the latter since there is a capacity for storing food in the body dêpots and moreover food continues to be absorbed for a long time after a meal is taken, so that although hunger is periodic in occurrence there are considerable intervals of freedom from the sensation-complex. In the case of respiration, however, it is possible to produce cessation of breathing as, by taking a rapid succession of deep breaths, forced apnoea ensues; in other words by removing the stimulus to breathing through over-ventilation of the lungs (causing a drop in the alveolar CO_2 content and a thorough aeration of the blood) the urge to respiration is temporarily suspended and it would be fair to assume that such storage of a necessity of life is the only essential difference between food ingestion and respiration. It will be recalled that nutrition and oxygenation in the foetus in utero are both continuous, and, just as the impulse to breathe does not arise, we may assume that the urge of hunger is equally in abeyance.
Hoelzel holds that one might regard hunger, if a sensation at all, as general and non-localisable and so, on this assumption, considers that it only differs from appetite in that the latter is mild hunger plus taste-memory processes. Apparently this view of hunger is comparable to the sensation of thirst in being a vague and general one, although the question of appetite does not arise in connection with the ingestion of water.
Stiller considered appetite was the sensation of hunger plus taste- and smell-memories of food and therefore maintained that hunger could occur without appetite, but not appetite without hunger. We have evidence to the contrary, however, as regards the latter assumption, for the over-feeding which occurs in those consuming tasty dishes can be attributed to the fact that appetite is a very untrustworthy factor in deciding the amount of food which we actually require.
Still (F) criticizes the term "taste-memory processes" because it only indicates that hunger may be directed to particular foods by taste-memory and so explains nothing. He thinks that a "good appetite" is merely another way of saying "hungry for food".
Carlson emphasises the intermittent (periodic) nature of hunger but always seems to regard hunger sensation and hunger pangs as one and the same thing - evidently the periods of activity of the empty stomach, in some cases, and possibly that of the small gut, accentuate the sensation of desire for nourishment, but evidence exists which throws some doubt on this view and will be mentioned subsequently.

Normally hunger and appetite are experienced together at the same time and the prominence of appetite in consciousness is possibly determined by the degree of the more important factor of hunger - if the latter is urgent, appetite takes a secondary place. It has already been stated that in the life of the normal individual strong hunger is never felt owing to the fact that food is plentiful and easily accessible without the necessity of having to search for it, and as meals are taken at regular and comparatively short intervals before the tissues are exhausted, and often before absorption of food is completed from the alimentary tract.
Thus habit and appetite play the important part with regard to feeding in the usual way. It is only in those creatures who struggle for existence and know what it means to go empty that hunger dominates the processes of ingestion and in those animals palatability counts for little, necessity for much.

Appetite appears to prepare the way for the relief of hunger by the providing for the digestion of food, although hunger is the signal that food is necessary. It is the normal association of hunger and appetite which renders it difficult to consider the mechanisms as separate entities, but it is evident that the foregoing views point to the fact that there <u>is</u> a qualitative difference between the two factors, complex and interrelated though they are.

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Chapter III.

THEORETICAL CONSIDERATIONS of the GENESIS OF HUNGER.

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So far we have considered the problem from a largely biological point of view and have attempted to indicate how it differs fundamentally from the closely associated factor of appetite.
We shall now endeavour to review the various theories advanced concerning the causation of hunger before analysing the mechanisms involved in, and regarded as essential to, the production of the hunger sensation.

From what has already been stated the origin of hunger is a problem which requires careful consideration, and, as is to be expected in any study of common-place phenomena, it will be evident that the matter is one of great complexity. This is obviously because it always proves to be difficult to interpret subjective phenomena (or sensations), since the lower animals who probably experience discomfort in a primitive form are unable to express their feelings except by re-actions (objective phenomena) whilst man has universally found introspective analysis to be faulty owing to the distortion of facts by the emotions as Hart has pointed out.

Pavlov, whose views on the question of hunger receive full attention further on, recognises this difficulty and he rightly states that we have no justification for theorising as to what animals may think and urges that we should go back to physiological observations and facts if we wish to be scientific rather than imaginative.

It is clear that however complex the genesis of hunger, it must be of central or peripheral origin, or due to a combination of these elements.

If of central origin we must assume the presence of a "Hunger-Centre" or centres in the central nervous system which respond to various stimuli, metabolic, nervous or blood-borne.

If hunger has its origin outside the central nervous system, it presumably arises in response to sensory stimulation in the alimentary tract; or it may be comprised

of both and be regarded as a general sensation.

Dealing in the first place with views which favour a central origin of hunger, Magendie considered hunger wholly a cerebral mechanism in which changes in the state of the blood and tissues played no part - this observer based his theory mainly on the fact that hunger pangs and the feeling of weakness may disappear spontaneously without ingestion of food and apparently contradicted the fact of the periodic motility of the empty stomach.

Schiff, Ewald, and others maintain that hunger is of central origin but believe that a starvation-state of the blood stimulates the centre.

Pavlov postulates a food-centre and bases this largely on the fact that hunger is an inborn reflex (instinct) and shows that the special excitability of the organism by food is a phenomenon of the physiology of the Central Nervous System. He also discusses the rôle of conditioned reflexes in feeding.

Katz, Beck and Bayer emphasise the importance of certain external factors, whilst regarding the brain as being principally concerned with the origin of hunger.

Hoelzel regards hunger as being determined by central rather than gastric factors, and in support of this view indicates that excessive food ingestion so suppresses the desire for eating that when the motility of the empty stomach returns, the contractions give rise to purely epigastric sensations without a sense of hunger. Moreover, he produces evidence to show that gastric manifestations are mainly incidental to hunger.

The main objections raised to the central origin of hunger are that it does not explain the reference of the hunger sensation to the stomach or the fact that hunger may disappear temporarily by eating indigestible materials, and, furthermore, the periodicity of the sensation does not seem to be in keeping with a nervous origin. Further Luciani, Tigerstedt and others show that whereas in starvation a progressive depletion of nutrient substances from the body occurs, hunger should be expected to increase as long as food is withheld, but actually this is not so; hunger disappears in about three or four days, especially if water is not excluded.

Boldirev showed that, as time goes on, the stomach contraction-periods in starvation appear less frequently and last for a shorter time until in about three days gastric secretion becomes continuous and all movements cease.

Cannon has also pointed out that division of both vagi and splanchnic nerves, although isolating the stomach and small intestine from the central nervous system, does not prevent the animal from eating. It must not be assumed, however, that this proves hunger to be of central origin since appetite and not hunger may lead to feeding them. Moreover, eating may occur from psychic

reasons, after all nerves to the stomach and even the gustatory nerves are divided - in fact, to conclude that eating is the result of hunger is especially likely to be fallacious when animals are considered (as opposed to man).

Regarding the theories that hunger is essentially of gastric origin it may be said that many of the views are fantastic in nature but this is owing to the fact that experimental methods were in their infancy when some of the explanations were advanced, conclusions being merely a matter of surmise.

For instance J. Muller regarded hunger as a negative sensation arising from the empty state of the stomach. It is clear that after gastrectomy or division of both Vagi the individual should, on this assumption, experience continual hunger and this is contrary to facts.

One and a half centuries ago Haller attributed hunger to stimulation of sensory nerves in the stomach by inherent gastric contractions, i.e. by the physical irritation of gastric mucosa associated with gastric motility. He based this largely on the fact that the stomach in starvation is usually in a contracted state.

Weber favoured the theory that gastric contractions in conjunction with obliteration of the stomach cavity resulted in the hunger sensation, much as tenesmus and colic indicate activity in the large and small gut respectively. These gastric contractions have been demonstrated experimentally by Cannon and Washburn, Carlson and others who considered them to be the cause of the hunger sensation. This is based on the close correspondence which they found between the motility of the empty stomach and the sensation of hunger. Christensen does not obtain such a parallel between stomach movements and hunger whilst Wangensteen and H. A. Carlson have shown that complete excision of the stomach in one of their patients left the hunger sensation unaffected. These latter observers agree that duodenal motility may still be a possible factor in the production of the hunger sensation and this view has been given full consideration and some support by Ivy & Vloedman, Quigley and Solomon and others, and in connection with the above it is of interest to note that the "hunger-pains" of duodenal ulcer, coming on, as they do, when the stomach and duodenum exhibit activity associated with their empty or relatively empty state and relieved, as they are, by the ingestion of small amounts of food, bear a close relationship to the sensation-complex of hunger. This will be considered briefly in connection with motor visceral phenomena.

Sternberg, rather fancifully, described hunger as "Pruritus Stomachi" and suggested that appetite was connected in some way with the oesophageal and gastric peristalsis.

That hyperacidity may be a factor in the

production of hunger, by undue stimulation of the sensory nerve-endings in the gastric mucosa, has been suggested but hunger may be present in a high degree when the stomach is entirely empty and it occurs also when HCl is absent (achylia). Hoelzel and Kleitman have noted sensations arising from stimulation by acid of the duodenal mucosa, but these sensations are not those of hunger but rather of appetite.

Against the view that hunger is of gastric origin are the facts that after excision of the stomach and Vagi the urge to eat still exists; also hunger may be experienced even when the stomach is partly filled with nutritive substances and, moreover, the sensation is partly relieved by rectal or intravenous feeding. The theory does not explain the urge to the first meal in the new-born.

In support of hunger as a general sensation we must mention the name of Bardier who holds that in the hunger state certain changes occur in the blood and organs of the body, and these alterations stimulate the theoretical hunger-centre directly (via blood) or indirectly (via afferent nervous impulses).

Mark and Wagner believe the condition of the blood has an important relation to the origin of hunger especially regarding the blood-sugar variations and Bulatao and Carlson have shown them to bear some relationship to the gastric hunger contractions. Many observers have noted changes in the latter following the injection of insulin.

Biedl believes hunger can be attributed to a hormone, and Tschukitscheff contributes to this theory by his experiments in dogs. He shows that the injection of blood from a starved dog, when its stomach is quiescent, increases the stomach motility of the recipient (dog), whereas if the donor's stomach is active the injection inhibits the activity of the recipient's stomach: these facts suggest the presence of a pressor and a depressor hormone. Luckhardt and Carlson had previously shown that phloridzin glycosuria in dogs increased gastric hunger contractions and that the injection of the blood of starved or diabetic dogs increased gastric motility of normal dogs.

Templeton and Quigley consider it possible that a hormone may be formed in the duodenum, when dextrose is present there, and which, when absorbed, results in inhibition of the empty stomach contractions.

Shur and Brugsch indicate that possibly the nutritive condition of the liver and muscles (food reserve dêpots) play an important role in the origin of hunger

whilst Muller regards blood changes in starvation, by stimulating the hunger centre in the brain, cause motor impulses in the Vagi to produce gastric contractions, but we know that double vagotomy does not affect the gastric hunger motility appreciably, which is primarily automatic.

Du Bois-Raymond postulated a Vagus hunger (of gastric origin) and a tissue hunger (the feeling of weakness) and the work of Busch in his classical case of duodenal fistula supports this interpretation of the problem.

Turro describes a "trophic reflex mechanism" of hunger whereby he attempts to show that nerve-endings in all viscera are stimulated by lack of food material and by this means impulses are sent to a "trophic centre" in the thalamus whence impulses arise affecting the higher centres (consciousness). Although he maintains that such an inherited mechanism is so functionally perfect as to lead animals to take in the correct amounts of necessary nutritive materials instinctively, we know that it is largely a matter of experience - trial and error - with various foods which ultimately gives us a clue as to our requirements. However, this theory is attractive because we are sometimes le d to wonder at the way in which people, quite ignorant of the principles of dietetics, manage to include all the necessary factors in their normal meals. But we have to face the unpleasant truth in saying that, too often, gross over-feeding is the means whereby sufficient quantities of the real essentials are ensured. Turro's hypothesis has been criticised by Carlson on the grounds that hunger may occur before absorption from the small gut is complete (before any starvation change in the blood is possible); moreover, even in prolonged starvation, chemical changes in the blood are not pronounced - but this does not mean that changes do not occur and possibly, in time, methods may be discovered which will enable one to show such alterations chemically. In addition to these points against the "trophic reflex mechanism" of hunger is brought forward the fact that indigestible substances and food (before it can possibly be absorbed) when introduced into the stomach cause temporary inhibition of hunger. It should be noted that if crystalloids are present in ingested fluids absorption occurs almost immediately from the stomach and so sweetened drinks may relieve the hunger pangs by their presence in the stomach, and following their absorption, the feeling of weakness (possibly allied to fatigue) may disappear also. Since hunger in man seems to decrease rather than to increase in prolonged starvation this has been raised as a point against the starvation changes in the body as being the main determinant of the sensation of hunger; that hunger

should be absent in fever when metabolism is increased with, possibly, prolonged starvation, might be considered as indicating that the depletion of blood and tissues does not cause the hunger sensation, but other factors e.g. toxaemia, enter into the problem in pyrexia; possibly the fact that if the lower centres connected with nutrition lie in the basal ganglia means that they would also be disturbed along with the heat-regulating mechanism in the thalamus.

Owing to the fact that hunger is commonly periodic in character, with sudden onsets and offsets, this is suggested as disproving the position of blood changes in its causation since they occur gradually and continuously, without sudden variations. However, as we shall see, the fact that there appear to be two kinds of hunger sensation - one associated with hunger pangs (gastric "empty" contractions) and the other related to a desire for food (and associated with respiratory changes as Hoelzel and Kleitman show) - makes it evident that Carlson possibly attaches too much importance to hunger as it is expressed by stomach motility.

Regarding the theory of the central genesis of hunger, Still quotes a view by Kuntz and Thoma - a depletion of nutrient substances in the circulating blood excites in some, as yet unlocalised, part of the brain efferent impulses which bring about reactions which, in turn, initiate afferent impulses resulting in the sensations of hunger. This mechanism, then, is analogous to respiration, which, as Pavlov shows, is a sound view.

One might compare the processes of feeding in the amoeba and man, regarding ingested food in man as still being outside the body virtually until it is absorbed into the blood-stream, just as the nutrient medium in which the amoeba finds itself is outside the organism. The urge for food concerns the organism itself and on that assumption the movements of the stomach and intestine, whilst subject to influences via the blood and nervous system of the organism, are primarily concerned with the processes of digestion; so visceral manifestations might be considered as of secondary importance in the sensation-complex of hunger.

Uneducated people, as Voit (quoted by Carlson) shows, for instance, Irish and Bavarian peasants whose meals consist largely of bulky starchy foods (potatoes and bread), when given diets of greater food value but smaller bulk, fail to be satiated; this indicates that hunger is, to a large degree, dependent upon the power of suggestion. The importance of this is brought out in the Two-Component Theory of hunger. This fact also demonstrates that the hunger sensation is not an indication

of the immediate need of nutriment due to starvation changes in the blood.

Perussé and Rozen have advanced an interesting theory relating to hunger. They suggest that the blood of starving animals, when exhausted of food substances, may contain metabolites which act on specialised receptor cells in the stomach (by lowering the threshold of irritability through lack of nutrient materials) and give rise to hunger contractions in this way. They maintain that there is not always a parallel between hunger contractions and the hunger sensation and point out that if powerful hunger contractions do not occur with the hunger sensation, the absence of the latter may be due to the effect of the metabolites on the central nervous system, whereby the gastric hunger motility is interpreted as nausea. In cases where the metabolites stimulate the stomach and not the central nervous system, hunger contractions may be interpreted as pain. If, when food is taken, the hunger contractions disappear the hunger sense should also go , but such is not the case and therefore empty stomach motility is apparently not the cause of the hunger sensation.

The views of Mulinos with regard to the persistence of hunger after the hunger contractions have been inhibited by food intake will be dealt with when the stomach activity is considered.

If we compare hunger with thirst we may find an explanation for it by analogy. De-hydration of the tissues occurs, including that of the mouth surfaces, and a dryness of the oral cavity results (which can be removed by cocainising the mouth) producing the distressing sensation of thirst. Depletion of the tissues in respect of nutriment leads to hyper-activity of the whole nervous system so that the threshold excitability of visceral sensation is lowered and thus the normal motility of the muscular alimentary tract (which can be arrested by ingestion of various substances) is appreciated in consciousness as an unpleasant phenomenon whereas usually, the visceral functions proceed imperceptibly.

Recently work on the vitamins suggest that a vitamin allied to Vit- B 1 or 2 may play an important part in the preservation of the normal urge to eat (Burack and Cowgill).

The above theories will be discussed more fully when the various mechanisms are studied systematically, but after considering the facts and hypothesis in the foregoing survey one inclines to the view that probably hunger pangs and the hunger sensation are distinctive though associated sensations and that the preponderance of either in consciousness is determined largely by individual

differences in the persons concerned. Before this interpretation can be made, it is necessary to study the matter in greater detail and to attempt to correlate the findings and their bearing upon the problem.

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Chapter IV.

SOME EXPERIMENTAL CONSIDERATIONS.

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Numerous workers have investigated the problem of the hunger mechanism by means of various experiments on animals and man.

Bernard, Sherrington and others have divided the gastric nerves (vagi and splanchnics) but found that this procedure did not destroy the desire for food, even when the gustatory nerves were also sectioned. This seems to show that hunger does not owe its origin to the stimulation of afferent gastric nerves although Cannon does not agree with this deduction. It has been shown that an individual may eat without either appetite or hunger, from habit or a sense of duty and, as the contributors to the Two-Component theory have shown in hens, eating may depend upon various factors psychological and otherwise. If an animal eats after section of both vagi it does not prove that appetite can be excluded as the cause since it is, as a memory process, a cortical phenomenon and neither does it show the effect of hunger as the causative factor. It is known however that section of the vagi prevents the production of psychic or appetite gastric juice.

Experiments in which the vagi or gastric mucosa are cocainized usually show that a disinclination for food temporarily results, but this work of Valenti has been criticised by Muller who shows that cocaine by the mouth does not affect gastric hunger contractions although it inhibits the hunger sensation, due to the effect of lack of nourishment, presumably by its affect on the cortex after absorption.

There is no doubt but that patients after gastrectomy do feel hunger just as before the operation and this has been thought to have been due to the fact that since, technically (as most surgeons agree), total excision of the stomach is almost impossible, sufficient cardia remains to secrete HCl and to dilate subsequently and exhibit hunger motility. Even, however, after total gastrectomy and double vagotomy (Wangensteen) hunger may be experienced as before except for an increased frequency of the sensation resulting from the lessened capacity for a normal sized meal.

Perthes also records a case where, after almost

complete removal of the stomach, the stoma, being patent, allowed the undigested food to leave the hypermotile stomach practically at once and hunger occurred so frequently as to necessitate feeding every two hours.

Busch, after observations on an emaciated woman with a duodenal fistula, concluded that the hunger pangs, which were present even when much food was in the stomach, were relieved by introducing food into the stomach, whilst her hunger was partially relieved by re-introducing the chyme, lost through the fistula, into the duodenum. Owing to the fact that the patient had a thin abdominal wall he was able to observe irregular periods of alternate rest and activity in the gut. These facts le d him to make a suggestion which is of outstanding importance and appears to be one of the earliest contributions to the idea that hunger does not arise wholly from visceral activity. He maintained that his experiments demonstrated a dual factor in hunger, namely, a condition of the central nervous system arising from tissue starvation, and an element due to the stimulation of nerves in the alimentary tract. As will be seen this view receives a great deal of support in the light of more recent work on the subject by Hoelzel and others. It must be admitted however, as Cannon points out, that the restoring of the chyme in relieving the hunger sensation may have acted by altering the nature of gastro-intestinal activity by means of its bulk; the importance of bulk of ingested food has been shown by Voit, as seen in the previous chapter.

Nicolai observed that hunger could be abolished temporarily by the act of swallowing or by passing a stomach tube (i.e. a part from the ingestion of food) and this was termed by Langley "receptive relaxation" of the stomach, being regarded by him as an instance of reciprocal innervation of antagonistic muscles reflexly controlled by the vagus nerve. Even water, saline, or indigestible substances passed via the tube into the stomach produce such an inhibition of hunger contractions for shorter or longer periods by a local reflex from gastric mucosa to gastric muscle. Pavlov showed that on masticating or swallowing food impulses passed down the vagi producing an associated "psychic secretion". Nicolai was le d to the opinion that appetite and hunger were qualitatively different factors and considered that either sensation could be felt apart from the other.

Cannon has attempted to show that a "psychic tonus" as well as a psychic secretion occurs on ingestion of food but this view has been disputed by other workers. He quotes the fact, recorded by Spallazani, that if a hen, starved for a day, was given nuts to eat, no movement of the stomach occurred so long as the organ contained only a few nuts, but it became active immediately when full.

This is of interest when the work of Christensen is dealt with where he points out that a certain minimal gastric content (food and gastric secretion) is required to maintain the human stomach at rest.

Schlessinger in feeding normal persons rectally for varying periods showed that, despite a gain in weight, these individuals were not entirely free from the hunger sensation. Carlson suggests that even such inhibition of hunger as was present may have been due to an inhibitory reflex mechanism from the rectum and colon to the stomach; distention of the rectum with water may produce reflex gastric secretion which may lead possibly to inhibition of gastric motility. But again Schlessinger's findings might be regarded as proving that whereas the supply of nutriment abolished the feeling of weakness (tissue-hunger) since the persons put on weight, yet the empty stomach contractions were still present and were felt as hunger pangs, being determined largely by a local mechanism, namely, the absence of gastric contents. The former observer found that if a person were fed rectally and the gastric mucosa were anaesthetised hunger disappeared completely, but whether the cocaine acted on the mucosa itself or on the plexuses of Auerbach and Meissner or centrally inhibited the sensation of hunger was not determined. From these experiments. however, Schlessinger concluded that hunger had a double origin namely peripheral (or gastric), and central by stimulation of a hunger centre by starvation-blood —a view which Du Bois-Raymond favoured.

Boring is of the opinion, after the subjective analysis of the character of the hunger sensation, that it is made up of pressure and pain elements - the former a variable, rhythmical, kinaesthetic sensation referred to the stomach and the latter a dull ache or gnawing pain in the epigastrium. When the kinaesthetic is referred to the throat and associated with salivation it is taken as showing the desire for food (appetite) - this is the sensory basis for appetite according to this psychologist.

Boldirev first showed, by means of balloons in the stomach of dogs, that during starvation the viscus undergoes periods of motility and quiescence and these alternations of gastric activity are associated with similar movements in the gut. He showed that a contraction-period lasted for twenty to thirty minutes (containing ten to twenty contractions) and quiescence followed, lasting one and a half to two and a half hours, when activity returned again, and he demonstrated that the motility of the empty, is greater than that of the digesting stomach, and quiescence was produced when copious gastric secretion occurred. Valuable as his experiments undoubtedly were, he, himself, failed to associate the active stomach with the origin of the hunger sensation and it is thought that

the fact that gastric motility gradually diminished after three or four days in starvation and the idea which he had that the central effects in starvation determined alimentary activity (via the vagi efferent fibres), led him to overlook the connection.

Haudek and Stigler state that the stomach empties more rapidly with hunger than without, whilst Cannon and Washburn showed that the stomach possessed a greater tonus in hunger, and Carlson indicated that the tonus varied with the length of starvation.

Ivy and Fauley have shown that up to seventy-two hours, fasting produced a decreased emptying time of the stomach but that afterwards the tone is inhibited by various factors - nausea, weakness etc. They also quote the work of Lorenzi who, by means of feeding patients with thyroid extract, shortened the gastric emptying time by two and a quarter hours as compared with the normal rate of emptying for those individuals. These observers have also produced shortening of the emptying time of the stomach, associated with polyphagia, by pancreatectomy and ligation of the pancreatic ducts. This work is of the utmost significance because it shows clearly the effects upon gastric motility of metabolic changes unaccompanied by the secondary effects of disease, and moreover, the results have been compared with the activity of the stomach in the same subjects normally.

Cannon and Washburn showed that in man the periods of empty stomach contractions are synchronous with the periods of hunger sensation and furthermore that each contraction is simultaneously associated with a hunger pang. An associated motility in the lower third of the gullet with empty stomach contractions have been shown by these experimenters who hold that the synchrony of gastric motility and the hunger sensation proves that hunger originates from a gastric mechanism. Carlson confirms these findings but admits that the proof of the genesis of hunger is not necessarily absolute whilst Christensen in a number of careful experiments on the relation of stomach motility to hunger does not agree that gastric hunger contractions and the hunger sensation occur together; in other words, he fails to confirm the existence of the so-called "hunger" contractions although he agrees that the empty stomach exhibits periodic motility, but attributes the sensation of hunger, in association with such movements, to suggestibility on the part of the experimental person. The latter probably becomes aware in time of the contractions as vague sensations but associates them with hunger only because he is actually deprived of food. Christensen moreover states that hunger may occur apart from hunger contractions and may not be felt when the latter occur.

Mulinos suggests that hunger is not removed by the inhibition of the hunger contractions and considers that the quiescent period following the ingestion of food is but the first phase lasting 1-2 minutes, the second being a period of increased activity which lasts for half an hour and which subsides suddenly to give place to digestive motility. Whilst the initial quiescence following food intake is a reflex inhibition from the mouth and gullet, the second motile phase is only seen when food (e.g. meat and moistened bread) is taken and so this phase would not occur with indigestible substances; and neither can it be inhibited by taking more food as would the hunger activity of the stomach.

Perussé and Rozen also point out that, since hunger contractions are inhibited when food is taken, the hunger sense should also disappear but as this does not occur the hunger contractions are therefore not the cause of the hunger sensation. Carlson maintains that hunger motility causes a sensation of hunger by the stimulation of afferent fibres of nerve plexuses in the wall of the stomach and not in the mucosa, and shows that the empty stomach motility is independent of the central nervous system and is a primary automatic gastric mechanism. It is clear that the empty stomach does exhibit periodic movements alternating with quiescence, but in animals the relation of this element to the genesis of hunger cannot be established because obviously the latter, in being a sensation, cannot be expressed by animals.

Johnson and Carlson have shown that an increased amplitude of the knee jerk occurs during a hunger period as well as during individual contractions and that also borborygmi and the passage of flatus may augment the reflex. Thus in a state of hunger the alimentary tract exhibits increased activity and the reflex excitability of the nervous system is also augmented, suggesting a common origin for the phenomena, namely the removal of cortical inhibitory influences. That the motility of the empty stomach produces the hunger sensation seems unlikely on the face of it, and we could equally well argue that the hyperexcitability of the central nervous system leads to the interpretation of empty stomach motility as hunger pangs - in fact, the findings of Hoelzel and Kleitman, who postulate an increased respiratory rate, more especially in relation to protein starvation, seem to support the view that the importance of the stomach movements in producing, rather than accompanying, the hunger sensation has been over-estimated. The two latter observers have shown that in starvation there appears to be an increased sensibility of the alimentary mucosa, and this is of interest when considered in conjunction with the above suggestions.

Whilst it is true that discomfort as fundamental as pain, hunger, or fear in time produces a hyper-sensitiveness to various sensations it is also of interest to observe that there appears to be a corresponding loss of cortical control, the change varying greatly in different

persons and depending upon judgment, will etc. For instance, as in moments of great fear we may appreciate the faintest of sounds clearly and even lose control of the sphincters so in hunger we respond readily to internal stimuli, e.g. impulses from the stomach of which we are not normally aware, and exhibit a raised nervous excitability, which in the more primitive animals would be shown by an urgent search for food.

Reference has been made earlier in this chapter to the fact that section of the gastric nerves affects neither the motility nor the sensation of hunger. The former result merely indicates that the contractions of the empty stomach are initiated in the stomach itself, but that hunger should be felt and the desire for feeding remain indicates that the contribution of the gastric element to the causation of the hunger sensation is mainly a subsidiary one. As we have seen, the factor which leads to eating after double vagotomy may be appetite, hunger, sense of duty, habit etc., but in isolating the stomach from the central nervous system we at least exclude afferent and efferent gastric impulses and leave the blood as being the sole means of communication between it and the rest of the body. That influences reach the stomach via the blood and affect its motor and secretory activity in various ways has been clearly established and these factors will be referred to subsequently in greater detail. It may be stated, however, that substances in the blood which tend to abolish the hunger sensation also tend to inhibit the motility of the empty stomach although we have no evidence which leads us to suppose that the alteration of gastric activity is primary and the affect on hunger secondary to it. It will be agreed that blood influences are more primitive than nervous impulses and play a more important part in nutrition than nervous factors, but this does not prove that the blood itself is the origin of the factors which produce the urge to eat. It does, however, tend to show that the blood is more intimately related to influences which lead the organism to eat than the nervous impulses and when substances are given which normally occur in the body e.g. insulin and thyroid, and which presumably normally affect food ingestion, the changes which follow are effected largely through the blood.

The view that blood possesses "hungry" qualities in starvation seems to be proved by its injection into other animals, as we have seen, but again the hungry blood may merely reflect the activity or needs of the tissues in containing metabolites which direct the activities and attention of the organism towards food.

There is a great deal of evidence which goes to show that hunger may be largely controlled by endocrine influences. Mention has been made of the work of Lorenzi,

Ivy and Fauley and others in connection with thyroxin and insulin. Perussé and Rozen have shown that in Graves' disease increased heat production must be met by an increased food ingestion in order to spare the body tissues and have shown how dextrose effects this especially.

Bulatao and Carlson have experimented with animals and by injecting glucose inhibited empty stomach motility, whilst insulin increased the contractions.

Templeton and Quigley found splanchnicotomy augmented the inhibitory effect of glucose (by the mouth) on hunger contractions and they suggested that glucose acted by producing, on absorption, a substance which depresses motility; or a hormone may be produced in the duodenum by the presence of dextrose in that part of the gut. These workers also obtained duodenal activity following insulin injections which preceded the gastric response and which occurred at times apart from the latter and which gave rise to a hunger sensation.

Wierzuchowski has studied the influence of various factors on galactose - assimilation in dogs, including hunger and insulin, and showed that the former in no way affected this whilst the latter increased it.

Tschukitscheff found that secretin and the end products of proteolytic digestion inhibited the hunger contractions of the stomach - the latter being of special interest in view of the type of hunger associated with the respiratory changes in protein starvation, as shown by Hoelzel and Kleitman.

Mark and Wagner showed the effect of hyperglycaemia in dogs as regards ingestion of cane-sugar and showed that when the blood-sugar level was kept down with insulin the dogs ate the proffered sugar ravenously despite large amounts of sugar in the intestines, whereas when the blood-sugar was high they refused the sugar. In diabetes in man, the need for sweet foods may be great despite the presence of hyperglycaemia because there is virtually starvation of the tissues in the midst of plenty owing to the inability of the person to metabolise the carbohydrate.

Schur regards the food reserve depots as the objects of metabolism and as the starting point for stimulation of the hunger centre in the brain and quotes Busch's case of duodenal fistula as indicating that the filling of the stomach is not the cause; he emphasises the importance of the clumps of proteins in the liver cells after meals.

Berkman, in showing anorexia nervosa to be

associated with a low basal metabolic rate, points out that professional starvers show a lowered metabolism not traced to a lowering of body protein or that of the body generally but owing to an innate protective mechanism. Their failure to return to normal soon after food ingestion suggested that the nutritive state of the body and not the influx of food decides the height of metabolism. He regarded hunger as being an inherent craving of the body for nourishment which is linked up with fundamental metabolic factors.

E. and S. Thyselius-Lundberg have recently shown the affects of tobacco-smoking on the blood-sugar curve and show that well marked rises may occur immediately which persist for half an hour, such a rise varying from 15 to 50%. The mechanism is believed to be by means of the liberation of adrenaline following the stimulation of the suprarenals by nicotine. It is a common observation that hunger is relieved by smoking,and possibly inhibition of the hunger contractions of the stomach occurs simultaneously.

Hoelzel and Kleitman have shown that protein starvation, as opposed to carbohydrate starvation, is accompanied by an increase in the respiratory rate and is relatively independent of empty stomach motility: the hunger sensation differs from hunger related to tonus variations in the stomach, which probably expresses a carbohydrate deficiency in the body, in being more diffuse and less clearly defined in its onset and offset. This latter sensation was essentially a "famishing" feeling whilst, as Hoelzel noted, ordinary hunger seems to indicate more a state of emptiness in the stomach - both sensations involved a desire to ingest something, in the former instance nourishing food, and in the latter instance any non-nutritive material which would allay the hollow feeling. They attribute this hunger sensation to the action of acid gastric contents on a hypersensitive duodenum and indicate that an increased sensibility of the alimentary tract is a feature of protein deficiency of undernutrition.

The above authors are inclined to the view that hunger occurs for the individual essentials in the diet and show that whilst hunger associated with the respiratory reflex indicates possibly a protein lack, the gastric hunger contractions and tonus variations reflect a carbohydrate need mainly. The hunger sensation is therefore a complex of specific urges and this hypothesis appears to agree in many respects with Turro's theory of the genesis of hunger.

Hunger is apparently determined by a host of factors which can be shown experimentally to affect gastric motility, gastric acidity, metabolism, etc.,

and which normally act together in order to ensure the welfare of the individual in so far as the urge for food is concerned.

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Chapter V.

HUNGER AND ASSOCIATED OR CORRELATED CONDITIONS.

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Many observers have noted the relationship of hunger and thirst and it is a fact that there is a close association between the two phenomena. Without, in any way, attempting to discuss the problem of thirst it is well to bear in mind that lack of water is much less well withstood by the body and less well tolerated by the individual than lack of food. The biological necessity for oxygen is even greater than that for fluids and so hunger occupies a position of lesser importance than either thirst or lack of oxygen, as regards the more immediate nutritional needs of the organism.

Starvation or professional fasting can be continued for long periods, (30 or 40 days) provided that water and salts are not excluded and, as we have stated, hunger, in disappearing after three or four days, does not cause any great discomfort; but this is far from being the case with the deprival of water - the agonies of thirst continue to the end. Hunger-strikers are in no way martyrs and seldom omit to take water because they know that little comfort results from sympathy, if death is the termination of their efforts.

Mention has been made of certain other physiological accompaniments of hunger and these can be briefly considered here.
In the first place it is associated with an increased excitability of the central nervous system and, as Carlson and Johnson have shown, this is expressed objectively by an increased amplitude of the knee jerk, which is shown not only throughout the hunger period but is evident with each hunger pang (or contraction of the stomach). The borborygmi and passage of flatus seen in hunger also appear to augment the knee jerk. Satiety depresses the knee jerk and may be associated with sleepiness.
The close association of hunger motility and augmentation of reflexes indicates that the former may be the cause of this condition. However, the increased excitability of the central nervous system may be compared to the augmented motility of lower organisms in the hunger state. Stimulation of the gastric mucosa (e.g. cold water via the stomach tube) augments the knee jerk.
Weygandt (quoted by Carlson) shows that dreaming during

sleep is more apt to occur in starvation - but this is also true after the taking of heavy meals before retiring. H. Weber explains Weygandt's claim by pointing out that since strong hunger contractions tend to disturb sleep, their inhibition when dreaming is excessive, suggests that the dream is the guardian of sleep and so Freud's view is supported on physiological grounds.
The increased excitability of the central nervous system may be further made apparent by subjective phenomena - headache, irritability, and failure to concentrate, and by restlessness.

Since hyperexcitability of the central nervous system occurs in hunger motility of the stomach, it must be an essential condition in the hunger state. The fact that the increased excitability is partly subconscious, since it occurs in decerebrated animals (Rogers and Goltz), is of interest since H. Weber believes it is related to the unconscious. Carlson points out that "the degree of the central effect varies with the intensity of the hunger contractions, the irritability of afferent nerves, and the stability of the central organisation". During hunger pangs the pulse is accelerated in proportion to the strength of the contractions and varies by an increase of 10-30 beats per minute. There may be an associated vaso-motor reaction indicated by an increase of the arm-volume (shown with the plethysmograph). It is uncertain whether the above changes are produced reflexly or by the interaction of gastric vagus and vaso-motor nuclei either directly or through the medium of consciousness, but since the vaso-motor centre is notoriously susceptible to various afferent stimuli these results must be regarded with caution.
Salivation has been shown by Carlson to occur in hunger, the rhythm of the flow of saliva being closely related to the hunger contractions and increased by the added element of appetite, but independent of the latter. This is probably a reflex phenomenon from sensory gastric stimulation related to hunger motility and may be a factor in the nausea sensation occasionally seen in marked hunger; whether salivation or nausea occurs, probably depends on the degree and nature of nervous stimulation in the stomach-wall viz. nerve endings in mucosa, submucosa or muscularis.
The feeling of emptiness is probably, in being a continuous sensation, merely an indication that the individual is aware of the fact that his stomach is devoid of content (but it may contain considerable amounts of gastric secretion) and this sensation, probably, is a central phenomenon without any actual local mechanism to account for it. Any counter-irritation of the abdomen may effect a change in this sensation e.g. pressure. The occurrence of borborygmi has a suggestive value in this feeling.
The sensation of weakness (allied to fatigue) may be due to actual lack of nourishment in the tissues and is of uncertain origin - it is a general sensation and may be

abolished by the mere act of taking food, which implies that a reflex or central element contributes to the condition. Busch's experiments suggest that the element of weakness in hunger depends on absence of absorption of nutrient materials and so it appears that this component increases in importance as starvation continues, finally to prostrate the organism from exhaustion.

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Chapter VI.

THE MOTILITY OF THE EMPTY STOMACH.

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The three main methods used in investigating empty stomach motility are:-

(1) by means of placing rubber balloons in the stomach connected with manometers whereby a tracing of pressure-changes may be made;
(2) by X-raying balloons in the stomach coated with opaque substances;
(3) by direct inspection of stomach movements via gastric fistulae.

Boldirev first investigated gastric motility in starvation in dogs by means of gastric fistulae and balloons and showed, as we have seen, that for the first three or four days the stomach exhibited periods of alternating activity and quiescence. The intervals of rest between the rhythmical contractions he regarded as being absolute in character although Cannon and Washburn showed that the stomach in man in the quiescent periods still exhibited tonus; they also associated the activity with hunger sensation, believing the former gave rise to the latter.
Carlson used the balloon-manometer method and showed that four types of rhythm occurred in the empty stomach:-

(a) periodic powerful rhythmic contractions (thirty-seconds rhythm) alternating with relative rest.
(b) tonus rhythm - from tonic fundus contractions (twenty-seconds rhythym) occurring during quiescence, so-called.
(c) pulse-pressure
(d) respiratory-pressure } rhythm is always present.

The periodic contractions correspond to the "hunger" contractions of Cannon and Washburn, and each may so increase in amplitude as to end possibly in tetanus - a condition where a second contraction appears before the first has disappeared.

The contractions have been classified into types depending upon their relative strength (Types I, II, III,). The contractions usually last for 20-30 seconds with 2-5 minute intervals at first, later running one into the other towards the end of a contraction period. A contraction period may last from $\frac{1}{2}$-1$\frac{1}{2}$ hours and is followed by quiescence of $\frac{1}{2}$-2$\frac{1}{2}$ hours' duration normally. Occasional 'spontaneous' stomach movements may occur but are atypical and unimportant.

Gastric "empty" motility, occurring as it does in the premature or newly-born child, is to be regarded as an inherited mechanism and the empty stomach activity appears to be influenced only by frequency of feeding and the amount of food given, both of which factors, however, are largely determined by the inherent motility of the stomach. In other words, whilst in the infant frequent feeding appears necessary, in time meals at less frequent intervals can be given since in the adult the degree and frequency of the contraction periods show a marked diminution (this latter change is most marked in old age), whilst obviously the capacity of the stomach increases correspondingly.

Gastric motor activity varies in different animals - in herbivora the stomach is normally never empty and feeding proceeds continuously; digestion activity merges into hunger activity and in starvation the contractions tend to end in tetanus. These facts seem to indicate that in herbivora the minimal gastric content required to produce hunger is high and in starvation these animals sometimes eat their own fæces, possibly to make up the bulk of gastric content.
In carnivora, however, the minimal amount of food in the stomach, before hunger appears, is apparently much less. These facts indicate that the type of food (carbohydrate, fat, or protein) is important in considering the question of hunger because obviously, if carnivora, who eat protein and fat, do not require to eat continuously to avoid being hungry it may be accounted for by the kind of food which they eat as compared with herbivora whose main food is carbohydrate. It will be seen that foods, rich in protein and fat, take a longer time to leave the stomach than carbohydrates and whether these delay the onset of hunger by producing a (digestive) quiescence in the stomach or by taking a longer time to be absorbed and so ensuring gradual repletion, remains to be proved.

In consideration of empty motility of the stomach in man one is naturally led to contrast this type of activity with that of digestion contractions in the relatively filled stomach.

Rogers and Hardt sought to investigate gastric motility by means of X-raying bismuth-coated balloons in the stomach. They found the fundus quiescent immediately after a good meal was taken, whilst tonus variations occurred directly or in about half an hour after food, depending upon whether a small or large meal was taken. Furthermore, they noted that when the stomach was nearly empty such tonic contractions were replaced by stronger contractions i.e. a slow tonus rhythm (made up of waves lasting 1-3 minutes) which increased in strength to terminate in "empty" contractions. Empty contractions consisted of powerful peristaltic waves

arising from the region of the cardiac sphincter and involving the whole stomach.
During the process of digestion the fundus acted as a reservoir exhibiting a tonic grasp upon the food which, when in contact with the cardiac end of the stomach, initiates contractions. Normally digestion and hunger contractions merge one into the other, the former mainly concerned with the pyloric end of the stomach and the latter possibly involving the entire viscus.

Cannon's suggestion was that the stimuli which led to a psychic secretion of gastric juice (as described by Pavlov) at the same time produce a 'psychic tonus' (increase of tonus and contractions of the stomach) which induces or augments the gastric hunger sensation. This he showed by cutting the vagi before and after ingestion of food - whereas in the former instance the gastric contractions are not normal (as shown by X-rays), in the latter instance the contractions, once started, continue unaffected. This hypothesis was disproved by Carlson who showed that stimulation of the gustatory end-organs, mastication of any substances, swallowing movements, and introducing various materials into the stomach, which normally stimulate the appetite, produce an inhibition of empty stomach motility.

Mulinos points out the common experience of the augmentation of hunger and appetite by the taking of food, whilst recognising the accuracy of Carlson's findings with regard to gastric motility, and states that the increased desire for food is suppressed when eating is continued to satiety or if, after an inadequate meal, half an hour or so is allowed to elapse. His experiments show that after ingestion of small amounts of food the sensation of hunger is increased, owing to a raising of the tone and the activity of the stomach, the latter disappearing if sufficient food is ingested or if a sufficient interval is allowed to elapse after the inadequate meal. This observer using balloons in fistula dogs showed that the inadequate meat meal produced immediate inhibition of the gastric hunger contractions and a fall in tone proportionate to the previous activity of the empty stomach; this was followed by a gradual rise of tone to a high level along with the appearance of sharp, frequent, irregular contractions - a period of activity which lasted for half to one hour and suddenly ceased. This phase was shown to be independent of digestion since practically none of the meal was digested or had even left the stomach, and thereafter, following the sudden fall of tone and activity, a quiescent period set in with rhythmic tone variations (as Carlson described), which lasted for about three hours.
Thus is shown an empty stomach phase and a pre-digestive phase connected with the gastric hunger mechanism, the

former activity being inhibited by food and the latter, having been initiated, being unaffected by more food and in this respect simulating the digestive phase, as was experimentally shown.

Rogers and Martin in an X-ray study of gastric hunger motility in healthy men conclude that it is a mixture of at least two types of activity-hyperperistalsis and circular (tonic) contractions of the antral end of the stomach and show that the different types of hunger contractions vary in intensity whilst the contraction is felt most when the lumen of the lower portion of the stomach is completely obliterated by the contraction, suggesting a pyloric origin of the hunger contraction.

Templeton and Johnson show that in the early stages of digestion peristaltic activity commences at the transverse band - the corpus and fundus acting as a reservoir - but later the origin is progressively higher up in the stomach until ultimately at the cardiac sphincter. Such activity, as Rogers and Martin suggest, might be seen in an empty stomach. Using the three-balloon method these observers (T & J) showed hunger activity to be peristaltic and demonstrated that when hunger pangs are most intense the balloon in the cardia showed great tone and slight contractions whilst the lowest balloon (in the pyloric region) showed marked contractions with a relatively less important increase in tone. A one-two-three rhythm (as indicated by the position of the balloons) was kept up. The tonus increase, although involving the whole stomach, is rather more marked in the pyloric region than the cardia. If hunger is less intense only balloons 2 & 3 were involved and balloon 3 was never involved unless 1 & 2 were also. Each contraction starts as a slow rise of tone and ends in a definite contraction - the whole gastric tone is also raised which continues practically to the end of the hunger period and then suddenly falls to recommence another slow rise throughout the quiescent period.

The synchrony of contractions of the empty stomach with the sensation of hunger which was demonstrated by Cannon and Washburn led them to attribute the latter to the former. This they showed by obtaining a graphic respresentation of the gastric contractions with the balloon-manometer method and the experimental person recorded the sensation of hunger by means of a switch without seeing the manometric tracing. It was found that the contraction preceded the hunger sensation and was outlasted by the latter and so Cannon's view was supported by this fact, but the periodicity of the contractions, if one admits that they do cause the hunger sensations, cannot be explained so easily. The rhythmical motility of the muscular stomach-wall is either due to a primary inherent contractile property of the muscularis or is the result of some efferent nervous process, but how this

produces the hunger sensations is not readily shown.

Carlson has shown that Cannon's results can be confirmed and maintains that if strong contractions are absent, hunger does not result and, generally speaking, that the intensity of the hunger sensation is proportionate to the degree of the stomach contractions. However, although he states that in prolonged starvation even medium contractions may give rise to marked hunger sensations, on one occasion during starvation, when palatable food was brought near, an intense hunger sensation arose without a corresponding change in the strength of the hunger contractions. This shows how difficult it is to assess the value of subjective phenomena. Mention has been made of experiments by Christensen who fails to confirm the finding that empty contractions and hunger sensations are synchronous.

This investigator points out Carlson's admission that his experimental person occasionally felt hungry without feeling the contractions, which were actually absent too, and this suggests that the person felt the contractions invariably and associated them with the idea of hunger.

Hoelzel has pointed out that empty gastric contractions may not always be associated with hunger but in the presence of mild fever (100° - 102°F) the associated sensations were headache, nausea and epigastric distress (Rupp) and in cases of tuberculous toxaemia the sensations produced are restlessness, headache etc (Meyer). Whilst it is true that disease may modify the functional activity of vital processes in a complex manner, the above facts taken along with the views of Boldirev and Iwanow show that there is much evidence in direct conflict with the views of Carlson and Cannon. Boldirev has claimed that periodic empty motility of the stomach does give rise to sensations but not <u>hunger</u> sensations (and Anitschkow agrees with this view). Iwanow reports that in the majority of cases his subjects do not associate hunger with the contractions of the empty stomach.

The work of Hoelzel and Kleitman, which seems to indicate that there is in prolonged starvation an increased sensibility of the alimentary mucosa - as shown by the irritant action of substances normally not possessing such properties, tends to support consciousness whereas normally they are not perceptible. This will be considered later but at present one must attribute such increased irritability in starvation, as shown by increased motility and sensibility of the alimentary tract, to augmented excitability of certain nervous mechanisms in the stomach and intestines or to a condition of hyper-excitability of certain cerebral areas.

Although gastric contractions are said to cause hunger sensations, especially when of a tetanic character, tonus variations when well marked may, according to Carlson, give rise to hunger pangs. The importance of tone has been previously referred to (Mulinos).

If marked gastric contractions follow in rapid succession the hunger sensation is said to be more nearly maintained as a continuous sensation i.e. it lags behind the contraction and may almost run into the next motile stage; this continuity is seen when gastric tone is high, although even then the continuous hunger sensation is augmented by hunger pangs if gastric contractions are very intense.
It should be remembered that hunger does not appear immediately the stomach is empty of food, although it may exhibit empty motility, and therefore some other factor in addition to mere lack of gastric content is concerned in the production of hunger presumably. Nicolai and Beaumont testify to the above observations.

We have seen that hunger is intimately related to the metabolic needs of the organism and slight mention in the introduction was made of the fact that the intensity of the sensation is more or less proportional to the degree of metabolism displayed under certain conditions.

It is to be expected that hunger should be maximal in infancy and minimal in old age because it is obvious that there is a greater necessity for food at a time when growth is in progress, when heat-loss is greater (owing to a proportionately larger body surface), and when activities are marked as compared with that when the body-processes are feeble and activities restricted.

However, in addition to a greater metabolism in youth there is also a greater motility of the empty and full stomach and hunger contraction - periods are more frequent. The onset of hunger is, therefore, seen to follow fairly soon after feeding from the above causes and when the capacity of the stomach is taken into account the fact is still more readily appreciated. Since empty motility is seen in premature and in newborn infants, before any experience with food has been acquired, it is obvious that the motor activity depends on an inherited automatic mechanism in the stomach and its independence of nervous factors may be shown by isolating the organ from the central nervous system by the section of all nerves supplying it. That functional activity is high in the infantile stomach is shown by the tendency of hunger contractions to end in tetanus and this indicates that secretory and digestive activity is probably equally vigorous.

Patterson has shown that in premature pups there is a continual series of contractions in the stomach with-

out intervals of rest whilst in adult dogs periods of quiescence vary (with age) from one and one-sixth to three and two-thirds hours and so he advances the view that stomach activity is in direct proportion to age.

As an animal grows older a diminution in gastric activity in both the empty and filled stomach occurs, due probably to reduced gastric and general metabolism.

Comparing the motor quiescence of the infant's stomach lasting from ten to sixty minutes that of the adult lasts for one to three hours, and whereas hunger, after a full meal, in infants develops in approximately two and a half hours it takes from four to six hours to develop in adults.

The stimulation which results in contractions producing hunger sensations may involve mucosa nerve-endings or the nerves in the submucosa or muscularis, or may be the result of activity in Auerbach's plexus whereby the brain and muscular wall of the stomach are simultaneously stimulated. Whatever the mechanism it is significant that whereas when the mucosa of the quiescent stomach is stimulated mechanically this is appreciated in consciousness (but not as hunger) yet such stimulation of the empty stomach so as to produce strong contractions leads to a sensation of hunger. That is, hunger pangs can be produced artificially. One could, of course, argue that the contraction is appreciated in consciousness and is interpreted by the subject as a hunger pang, since he is hungry at the time - in other words, empty motility is naturally associated with hunger and not the cause of it and experiments in animals cannot help us in solving the problem. Carlson admits that the ability to recognise individual contractions as separate hunger pangs depends upon the individual and varies with experience being acquired by practise.

If the empty stomach is distended by means of a balloon a hunger pang results just as tension in voluntary or plain muscle caused pain (cramp or colic) and the sensation may presumably arise from the stretching of afferent nerves in the muscularis. The distention of the stomach by a full meal may produce pain and nausea but in such a case there is present a nocuous element; doubtless, in hunger where there is undue muscular tension (hunger contractions) the element of pain does exist apart from a kinaesthetic sensation. It is of interest to compare tension in a relaxed and in a contracted stomach with the activity of the rectum where one obtains a simple call to defaecation by the entry of faeces normally, whereas in the presence of a foreign body e.g. (a growth) tenesmus results.

There is an associated rise in tonus with contractions of the lower unstriated part of the gullet

when the empty stomach is active (Cannon and Washburn) but this activity is probably incidental and does not play such an important part in hunger as these two observers assert; indeed, the oesophageal motility may be due purely to a local reflex mechanism resulting from the presence of a balloon in situ and unrelated to gastric motor activity. That the cardia does take part in empty stomach contractions is shown clearly by the three balloon observations of Rogers & Martin and Carlson states that when a hunger pang is being experienced withdrawal of the balloon is rendered difficult, proving that a contractile condition at the cardiac orifice takes place.

The activity of the small gut in hunger has already been referred to in Chapter III, and at the present one would only add that Busch and Boldirev have both confirmed separately the fact that intestinal motility does occur in association with the hunger sensation and stomach movements. It will be remembered that Wangansteen and H. A. Carlson admit the possibility of the hunger sensation arising in response to duodenal activity only because in their classical case the stomach, being absent, could be definitely excluded as the cause. It appears that the ordinary methods of investigating gastric motility cannot be applied in the intestine since the presence therein of any recording apparatus produces a local reflex contraction which masks its empty motor activity.

The work of Alvarez indicates that increased motility of the stomach leads to increased motor activity of the whole gut and this is to be expected in hunger since visceral activity can be implied from the frequency of borborygmi in the hunger state. It is likely that intestinal activity does produce sensations which probably reinforce sensations arising from contractions of the empty stomach and so the fact that hunger was totally abolished by introducing chyme into the intestine in Busch's patient might possibly be attributed to modification of the motor activity of the gut.

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Chapter VII.

THE SENSIBILITY OF THE STOMACH MUCOSA.

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The question of the sensibility of the viscera is a matter of the keenest controversy and it is considered as being beyond the scope of this work to discuss the matter except in so far as it concerns the hunger mechanism. However, sensory nerves supply the stomach and their stimulation leads to local reflexes or produces subconscious central effects, whilst in certain cases sensations appear definitely to reach consciousness.

As regards the mucosa itself there is apparently an insensibility to painful stimuli unless the latter cause damage to the mucosa and so allow the submucosa to be irritated.

There seems to be a general agreement that pain is produced by "an increase in the contraction tension of muscle-fibre" (Bolton) and such a condition is present in spasm (contraction) or in distension of the stomach, however produced.

Since there is an undoubted element of pain in hunger pangs it seems reasonable to suppose that the latter arise, in part at least, from muscular visceral contractions (stomach and intestine) in association with their empty state. As to whether the hunger pangs form the sole or merely subsidiary portion of the complex hunger sensation is subject to discussion and presumably other factors also play a part in its causation.

So far, the stimulation of the gastric mucosa does not appear to contribute to pain, regarded from a physiological point of view. A similar absence of sensibility to tactile stimuli is apparent although Pavlov does not wholly agree with this but believes that there is some response to mechanical stimulation. Hoelzel and Kleitman attempted to prove the latter by the ingestion of a quantity of millet seed (first removing the residual gastric content) but found that thirst resulted and this lasted apparently until sufficient time had elapsed for the barely moistened seed to become thoroughly soaked with gastric juice. Thus, they believe that this fact postulates a gastric or duodenal component in thirst as opposed to the intestinal component, seen in cases of diarrhoea. Carlson's experiments point to the absence of tactile sensibility in the gullet and stomach. It is worthy of note that normally substances which appear to produce sensations in the stomach may do so by their action on

the duodenal mucosa as Hoelzel and Kleitman point out, e.g. HCl.

As regards temperature, the gastric mucosa appears to be sensitive to extremes of heat and cold (protopathic sensibility) - especially the latter - and this is in agreement with Head's experiments on the colon (colon lavages) but the possibility that temperature variations may be referred to the epigastrium from the oesophagus must be admitted.

Turning to the question of the sensation of fullness and satiety, the mucosa apparently is not responsible for this and the interesting experiments of Hurst show that the raising of the intra-gastric pressure to 12-14m.m. Hg. produces a sensation of fullness in the epigastrium which disappears when the pressure falls by 2m.m. (from relaxation of the tone of the stomach) but which can be restored by reproducing the former intra-gastric pressure. This shows that tension on the circular muscular fibres causes the "full feeling" and the importance of tonus is shown by the fact that in an atonic stomach the introduction of a mixture of bi-carbonate of soda and tartaric acid fails to produce this sensation of distension.

Noltenius believes that the retreating of the hunger sensation in fasting can be explained by the absence of the nervous reflex which is produced by taking food - viz. the distension of the stomach wall, which is now absent.

Satiety is a matter of largely psychological interest as the work of Katz, Beck and Bayer has shown. It seems that normally the amount of food ingested is determined mainly by our experience with nutrient substances, and whilst those lacking in judgment and ignorant of food values may exhibit a total inability to eat within reasonable limits, it is true to say that, generally, we all ingest far in excess of our actual requirements. This error results, as we have suggested, from the fact that appetite actually plays a more important part in feeding than hunger amongst civilised peoples - we have forgotten that our palates are aids and not guides to eating. Carlson points out that certain conditions must be fulfilled in order to result in satiety; thus, hunger or appetite, in some degree, must precede the taking of food, which should be palatable, and of sufficient bulk to cause a sense of fullness of the stomach, whilst cerebral factors (the memories of the taste and smell of food etc.) play the chief part in the condition probably.

In considering the gastric mucosa we are well aware that certain forms of stimulation produce a feeling of nausea or vomiting, but in most cases factors outside the stomach are involved. Physiological nausea is due to unpleasant sensory impressions associated with certain

foods or the memory of such unpalatable substances, but usually nausea has a pathological basis. Nausea therefore arises from normal stimulation of hypersensitive gastric mucosa or nocuous stimulation of the normal mucosa, due to gastric contractions (here a pressure-pain sensation occurs especially in association with pyloric contractions) or excessive stimulation of the mucosa (pain) respectively.

Occasionally hunger may resemble mild nausea, as Boring points out, but Carlson suggests that in such cases a pathological stomach was possibly not excluded in the experimental subjects. Boring has emphasised the kinaesthetic element in hunger, nausea being due to the stimulation of the mucosa. Whereas hunger intensifies appetite, nausea seems to counteract it. In vagotonia hunger may contain an element of nausea. Again, as Hoelzel and Kleitman have shown, the increased sensibility in starvation in association with hunger pangs may lead to the presence of mild nausea in hunger.

The latter observers have shown a specific sensibility of the digestive tract, already referred to, which gives rise to hunger sensations distinct from empty motility sensations (hunger pangs) and associated with an increased respiration rate. A sense of tension in the stomach appeared during this type of hunger, but neither gastric contractions nor tonus was responsible for this (with a balloon in the stomach to record gastric activity), and so the duodenum was suspected as being the origin of the sensation. Adjustments in the diet subsequently indicated the relation of this sensation to protein starvation, whereas fasting motility of the stomach, as will be shown, is mainly influenced by carbohydrate deficiency; the former hunger sensation occurs apart from gastric hunger motility but may be increased by it. The characteristic differences between this hunger sensation and hunger pangs has been previously dealt with.

Boring reported a hunger sensation produced by introducing 5 or 10% HCl into the stomach and Carlson mentions that appetite may be produced by introducing $\frac{1}{2}$% HCl likewise, and these observations led Hoelzel to investigate the problem and to conclude that acidity was in some way related to protein intake and gastro-intestinal sensibility and that the acid produced the hunger sensation probably by its action on the pyloric or duodenal mucosa. It has been noted that hunger and appetite occur even in the absence of free HCl in the stomach, as in achylia, and indeed with complete absence of the stomach.

The effect of protein and fat in neutralising or inhibiting the acidity of gastric juice is well known. The action of normal acid gastric juice has been thought to be by means of its effect on hypersensitive mucosa and

corresponds to the action of stronger concentrations of HCl on normal mucosa which Boring observed.

Facts which confirm the hypersensibility of the alimentary tract in fasting have been referred to viz. the irritant action of substances ingested which do not normally exhibit this property, the greater sensibility of the mucosa to mechanical stimuli (e.g. the recording balloon in the stomach) and the tastiness of food after long periods without nourishment (which we have all experienced).

Macleod dealing with the question of "hunger pains" in duodenal ulcer has produced pain in an ulcer patient by distending the duodenum with air via a duodenal tube. This may afford an explanation of the mechanism of nausea when hunger contractions are marked in a fasting person viz. by the forcing out of air into the duodenum which if having a hypersensitive mucosa would result in pain (as Macleod suggests in cases of duodenal ulceration) or some allied symptom e.g. nausea.

The relation of stimulation of the gastric mucosa to hunger will be dealt with in the following chapter when the nervous mechanism of hunger is discussed.

The inhibition of hunger motility by gastric juice depends on the amount of free HCl and on the bulk of the secreted juice. Since gastric secretion produces inhibition of empty motility but is associated with digestive movements of the stomach it is clear that these motor mechanisms, related to hunger and appetite respectively, are fundamentally different.

The introduction of alkalies into the stomach produces the same inhibitory effects as equal amounts of water, although regurgitation of duodenal contents is a normal phenomenon and may be even associated with a possible duodenal component of hunger, as Hoelzel and Kleitman indicate, provided the quantity regurgitated does not exceed the minimal amount required to produce inhibition by mere bulk.

Local anaesthetics have been employed in order to determine their effect on gastric hunger movements but they are not retained in the stomach and pass on before anaesthesia is produced. In any case, the central effect, in the case of cocain, renders the results difficult of accurate interpretation.

Alcoholic beverages increase appetite if taken before or with meals and, as Clarke states, this action is by stimulation of gustatory nerve-endings producing salivation and psychic secretion of gastric juice, secondly, by a direct action on the fundus causing a free secretion

of dilute gastric juice, and finally, by its central action disturbing emotions are inhibited. Since alcohol is readily absorbed it should be expected, when given in sufficient amounts, to act as glucose by relieving hunger, but probably if sufficient time is allowed to elapse before the meal is taken its results are similar to that of inadequate amounts of food (Mulinos and Pavlov). There can be no doubt that it does increase the sense of hunger up to a point, however. Alcoholic drinks when introduced in adequate amounts do produce inhibition of hunger motility for longer periods than water, presumably owing to their specific effect in increasing gastric secretion, and sour wines (which contain acids) again produce longer periods of inhibition.

CO_2 which stimulates many nerve-endings (e.g. in mouth, nose etc.) acts as does water, in inhibiting fasting motility of the stomach, and so inhibition is the universal effect of substances introduced into the stomach.

The autonomic nature of gastric hunger contractions is favoured by the fact that repeated single inhibitions (produced by re-introducing substances into the stomach as motility returns) may be undertaken so as to produce a $1\frac{1}{2}$ - 2 hours' continuous inhibition but it must be obvious that quiescence so induced is compatible with marked hunger despite an artificial removal of the hunger pangs.

Carlson suggests that his experiment shows the relative independence of hunger movements from blood and nervous influences although this is true, in part, the conditions of the experiment do not obtain normally and only involve a given period of time when blood-changes would be practically negligible. The effects of excessive intake of food have been shown, indicating a definite relation between the emptying time of the stomach and the reappearance of hunger contractions and the influence on hunger has been mentioned (Hoelzel). Nerve division in animals indicates the effect of nervous influences to which the gastric musculature is subject normally.

Double splanchnicotomy diminishes the inhibition, resulting from the introduction of substances into the stomach, since tonus and gastric hunger contractions which are normally expressed by sympathetic stimulating influences (well marked in emotional states) are released from the latter control.

Section of both vagi and splanchnic nerves depresses the local gastric inhibitory reflex but does not abolish it and this shows the inherent dependence of the latter on local nervous mechanisms, probably through the medium of Auerbach's plexus. However, complete isolation of the stomach from the central nervous system removes the long gastric reflex as a reference to Diagram A on page 54a shows. Rogers and Hardt have shown that, in man, the fundus tonus rhythm exhibited in digestive activity of

the stomach is relatively insusceptible to chemical stimuli as compared with that seen in fasting motility.

The role of chyme in modifying fasting gastro-intestinal activity has been implied by Cannon who bases this hypothesis on Busch's experiments in his case of duodenal fistula, and further Alvarez, in considering the observations of Boldirev, who maintains that acids in the small intestine tend to inhibit hunger contractions of the stomach whilst increasing the tonus and contractions of the gut, shows that it is possible that the latter may depress gastric motility during digestion and fasting. The intestinal activity is not only modified by chyme but also by the introduction of acids, fats and by mechanical stimuli in cases of intestinal fistulae.

The inhibition of hunger by smoking has been shown by Carlson who believes its action is mainly via stimulation of gustatory nerve-endings in the mouth and mucosa nerve-endings in the stomach.

The inhibition of hunger, he admits, is not wholly to be accounted for in this way although the inhibition of the hunger pangs is more or less in proportion to the strength of the tobacco, and he maintains that the deviation of attention by smoking with a possible splanchnic action from absorption of nicotine, completes the inhibition of hunger. He shows that inhibition of the hunger contractions continues throughout smoking and may outlast the latter by $\frac{1}{4}$ hour.

In view of the recent important work of E & S Thyselius-Lundberg who show that tobacco-smoking produces well marked rises of blood sugar (15-50%) immediately and which persist for $\frac{1}{2}$ hour it can be seen that there is probably a close correlation between the blood-sugar level and hunger which is brought into evidence by the mobilising of sugar by the above mechanism.

These investigators believe the blood-sugar variations depend upon the stimulation of the suprarenals (by absorbed nicotine) with a subsequent liberation of adrenaline and so the splanchnic inhibition which Carlson hinted at seems to be similarly explained.

Carlson has attempted to analyse the effect of "tightening the belt" in hunger and has shown that abdominal pressure of itself is insufficient on purely mechanical grounds to produce a decrease in hunger motility. The fact that tramps employ this method after meals which could, under better conditions, have been of sufficient magnitude to produce a sense of epigastric fullness (satiety) may explain why external pressure is used to remedy a defect in internal distensions and the action on hunger can be accounted for by central factors alone. The possibility of mechanical stimulation of the solar plexus and splanchnic inhibition of hunger motility therewith must however be borne in mind.

Lennhoff suggests that hunger pangs may be appeased by inadequate amounts of food when abdominal pressure by means of a belt is applied and he believes this to be due to an altered tonus of the abdominal muscles; there is little evidence to support the accuracy of such an assertion. Psychic suggestion along with the results recorded by Mulinos would account equally well for the relief of hunger by the application of abdominal pressure.

Turning to the question of the influence of exercise on hunger it is a common observation that vigorous exertion is unaccompanied by a desire for food (and may even produce the opposite effect of nausea) although hunger is subsequently stimulated in some way after the muscular effort is completed i.e. after an interval of rest.

Boldirev has shown that fatigue in dogs causes a failure of the hunger contractions to appear with a disinclination for food and this is true in the case of man who may be too physically and mentally tired to eat.

Crandall has shown that physical exercise in dogs also depresses gastric secretion, in addition to digestion movements, and this suggests that the energy of the organism is conserved except in so far as it is required for the task immediately at hand. Again this indicates the importance of carbohydrate in relation to hunger motility.

Carlson has demonstrated an inhibition of hunger motility during running which is proportional to the speed and when hunger motility returns (after resting) it exhibits an augmentation provided the exertion does not produce exhaustion of the individual. This fact suggests that animals who exhibit a like modification of hunger motility, require to be spurred on in active search for food but as hunger contractions (pangs) disappear the urge for food would then have to be accounted for by some element in hunger distinct from sensations arising from fasting motility.

The effects of the external cold whilst producing at the time, an inhibition of hunger motility, subsequently increases it and in addition causes a sense of well-being in the organism (e.g. effect of a cold bath). It is possible that the production of histamine in the skin, as the result of exposure, on absorption stimulates gastric secretion and so causes an arrest of hunger motility.
The increase of fasting motility as an after-effect of ½hr's intense cold is shown by a tendency of the hunger contractions to end in tetany, a condition otherwise not seen except after 3 or 4 day's starvation.
Carlson quotes Lusk in showing that such external cold may render the liver free of glycogen and this is probably the case in severe exertion as well, and therefore indicates increased oxidation in which carbohydrate metabolism plays a predominant part.

The mechanism of such increased gastric empty

motility as after-effects of severe exertion and intense cold is likely to be due to the stimulation by blood changes of the vagus nuclei (motor) with a tonic stimulation of the gastric musculature and if afferent impulses from the stomach muscle do play a part in this, their effect is thought to be mainly subsidiary. (Carlson).

There can be little doubt but that gastric afferent stimuli travel almost exclusively along the vagi but possibly intestinal impulses may travel via the splanchnic and spinal nerves in addition. After section of the vagi the long gastric reflex is abolished and psychic secretion of gastric juice ceases, but this operation does not appreciably interfere with eating as hunger can still be felt and gastro-intestinal motility continues but at a somewhat lower tonic level, since the motor activity of the alimentary tract is autonomic in nature.

Pavlov has shown that numerous nuclei are involved in hunger since the simpler mechanism related to feeding can be undertaken in the absence of the cerebrum whereas the more complex processes suggest centres in the cerebrum. As regards the lower hunger centres the sensory nuclei of the vagi (the central portion of the long gastric reflex) in the medulla (fasiculus solitarius) are associated with simple reflexes relative to food:- nausea, salivation, respiratory and vaso-motor fluctuations etc., but these functions do not involve conscious factors and so cannot be strictly regarded as being hunger centres, if by 'hunger' we mean a distinctive sensation.

The decerebrated pigeons which exhibited a conduct indicative of a need for food were able to ingest food despite their inability to search for nutriment or even to recognise the grain offered as food; but when the optic thalamus was removed the characteristic "hungry" behaviour is lost. This shows the importance of the basal ganglia in initiating activity related to depletion of food substances (hunger). Carlson and Boring, we recollect, suggested the protopathic nature of hunger pangs (based on the fact that they are associated with pressure pain sensations and are crude and not readily localisable) but this implies that a cortical connection is absent whereas there is every reason to believe that the cerebrum is involved. Sherren and Head support the view that hunger sensations are essentially protopathic and without direct relation to the cortex, as opposed to the most finely discriminating epicritic sensations associated with appetite.

This hypothesis points to a subcortical origin of hunger whereas the more recently evolved appetite complex has cortical connections. The recognition of certain sensations occurs in the thalamus e.g. pain and discomfort, and coarse sensations of heat and cold. Hunger does not appear to be related to the special senses as is appetite but appears to be more closely allied to the fundamental emotions and so the subcortical end-station (as the centre for feeling) is favoured as being the virtual hunger centre.

As Head points out, lesions of the cortico - thalamic fibres cause an exaggeration of the feeling-tone accompanying sensation, and thus the greater the affective reaction to any stimulus the more certain is its connection with the thalamus.

H. Weber suggests that the possible close relation of the emotions and crude sensations to the thalamus supports the hypothesis of the connection of hunger to the unconscious. Destructive lesions of the thalamus may produce a disturbance of emotional movements without affecting voluntary movements of the face.

Carlson quotes the view of Schuller who states that the common occurrence of polyphagia in patients with pineal tumours may be due to irritation of the sub-cortical hunger centre.

The importance of the thalamus is clearly great, and one might expect to find in fever that impaired function of the basal ganglia would also be associated with a diminished hunger urge, despite a greater metabolic need for food.

The fact that the temperature in hibernating animals may fall to a point 2° above the freezing point in association with a loss of the hunger reaction, and possibly hunger sensation, still further supports the view that the function of the thalamus is normally closely identified with the sub-cortical mechanism of hunger.

The question of a cortical hunger centre may be considered in Chapter XI since Pavlov has adduced evidence, on original lines, to show the presence of such a centre, although he does not distinguish clearly between appetite, which has undoubted cortical connections, and hunger which may possibly have such relations.

The localisation of the cortical hunger centre or centres has not yet been ascertained although numerous observers suggest the part of the Rolandic area related to taste and the movements of mastication and deglutition as being a possible site.

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Chapter VIII.

HUNGER IN STARVATION.

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The question of the disappearance of the hunger sensation after 3 or 4 days' starvation has been dealt with and this circumstance appears to be related to the fact that at this time gastric secretion becomes continuous. If the gastric content exceeds a certain amount, as Christensen points out, hunger contractions will not occur and possibly this phenomenon might account for the loss of the hunger sensations. But hunger contractions may be seen after a 40 days' fast (Hoelzel and Kleitman) however.

We know of instances where faithful dogs may refuse food when their masters die, but normally, unless deliberate fasting is resorted to and, provided that man or animals retain the desire to live, deprivation of food is followed by active attempts to secure nourishment. Thus, although starvation is not painful or unpleasant after the initial period of lack of food, provided salts and water are obtainable, the known effects of continued failure to ingest food lead cerebral factors to activate the organism in order to procure the necessary nourishment.

The actual absence of the hunger sensation in the later stages of starvation may be due to acidosis or to great enfeeblement of the various constituents of the hunger mechanism, but before such profound changes occur the absence of hunger may result from a functional defect in some part of the apparatus normally involved in producing hunger sensations. The fact that hunger does not increase in prolonged starvation is sometimes regarded as evidence that it (hunger) cannot be due to the effects of tissue-changes unless some inhibitory factor arises, as the result of starvation, which interferes with the normal expression of tissue-depletion by producing an urge for food.

One might regard the disappearance of hunger after the initial stage in fasting as being due to the fact that the objective phenomena viz. gastric hunger contractions are in abeyance and therefore hunger pangs cease to be felt, whilst the hunger, regarded as an instinctive urge and closely allied to the urge to live, still remains as something essentially subjective.

Carlson found during a 5-day fast (water was taken and exercise and usual work carried out) that,

objectively gastric tonus and motility and frequency of hunger periods exhibited an increase and that a continuous scanty secretion of acid gastric juice occurred throughout. Subjectively, he noted that the general health, apart from mental depression and slight weakness towards the end of the fast, remained good, and whilst at first the hunger sensation was more marked than the gastric motility would lead one to expect, the reverse occurred later - the hunger sensation was continuous, punctuated by hunger pangs during gastric contractions. The burning epigastric sensation on the fifth day was attributed to acid stimulation of hyperexcitable nerve-endings in the mucosa, and Hoelzel and Kleitman confirm a hypersensibility of the alimentary mucosa in starvation.
Carlson mentions that during starvation, although hunger increases up to 3 days, it subsequently declines and gives place to nausea or aversion for food - this does not seem to be the universal opinion however.
Carlson confirmed the increased motility in the empty stomach of dogs up to 15 days of starvation while Luckhardt found that the above was exhibited in the case of two diabetic dogs and which continued to increase up to within a few hours of death despite marked emaciation and weakness.

Although an increase of motor activity occurs in starvation the lessened appreciation of this in consciousness was suggested by Carlson to be due to a depression of the central nervous system from lack of food.

H. Weber points out that the diminished conscious desire for food is designed to preserve the wasting of tissues (due to the absence of ingested nutrient material) which would be involved in a fruitless search for food. Thus the sensory threshold for hunger is raised after the initial period in complete abstinence from food.

The Cerebral effects of prolonged fasting have been referred to by Noltenius and the fact that fasting is resorted to, may in itself, imply an abnormal mentality of the subject. It seems unlikely that such elevation of cerebral activity would be exhibited by starving individuals (i.e. persons involuntarily deprived of food) and it is probable that the circumstances relating to the act of cessation of food-intake largely determine the nature of the mental or moral response.

If mental depression does occur in starvation, it, and most of the weakness, disappears after breaking the fast, which suggests the possibility that the former may be due to a reflex mechanism rather than to a depletion of nutriment in the blood (Carlson), although the cheering effect of a meal is still more suggestive of a psychic origin. It is obvious that any weakness remaining does not go for about 2 or 3 days but the sense of well being. afterwards, is very pronounced.

Various experiments have been undertaken which suggest that growth and metabolism generally may be stimulated by an occasional fast.

Hoelzel showed by means of an excessive food intake that the desire to eat was suppressed and that although gastric contractions did occur and could be felt (sometimes as epigastric colic due to gastric tetanus) as local sensations they did not give rise to hunger. He attributed this to the fact that the need for food was not present in sufficient degree, and in support of his contention quotes Carlson's observation that the first period of gastric hunger contractions after a meal were less prominent than later ones. Thus gastric empty contractions may be noted apart from hunger or may be interrupted by dietetic excesses.

If heavy meals in the evening are indulged in we commonly fail to feel hungry in the morning and as Hoelzel points out this may be partly due to the intervening sleep but can be accounted for by his experimental findings in over-eating.

This observer by eating easily assimilated food in the mornings found that hunger could be satisfied daily for months on end although insufficient was eaten to maintain weight or energy, and he cites these facts as showing that hunger is independent of epigastric sensations and makes the disappearance of hunger in prolonged starvation more readily understood. The sensations due to gastric motility in starvation are not constant and are not related to hunger despite the fact that the desire to resume eating exhibits a progressive increase; these results are the experience of Hoelzel who has fasted for prolonged periods. Professional fasters apparently still feel the desire to eat when exhibiting their prowess by refraining from eating and do not require to be coaxed unduly to eat when their fast has exceeded that of their rival.

If one chooses to regard eating as being largely due to an element of habit it would prove difficult to end this habit just as it proves difficult to give up the taking of drugs, but in the latter instance it is non-essential actually, whereas in the case of eating the element of necessity would still persist if meals were avoided.
Hoelzel suggests that hunger is more a motor than a sensory phenomenon and in this conception supports Pavlov's idea of hunger as a movement reaction towards food.

It is a striking fact that an infant at an early stage of life, when gastric empty motility is very pronounced, cannot interpret the latter as being unpleasant and yet exhibits an urge for food and drink both of which, Nature, in her providence, has arranged shall be supplied in an

ideal combination in the maternal milk. The means whereby such nutriment can be taken is seen in the sucking reflex which is inborn and the distress which arises from lack of nourishment must be non-localised presumably.

The motility of the empty stomach in starvation may be affected by emotion which, leading to a liberation of adrenaline, produces inhibition of motor activity of the stomach through its action on the splanchnic nerve-endings.

Carlson maintains that professional fasters may by hypnosis exclude hunger pangs from consciousness, but this psychic mechanism could as readily suppress hunger were it wholly of central origin and a continuous sensation, as Hoelzel holds it to be. The suggestion that hypnosis may induce hunger has apparently received some support when the experiments of Bayer with hens are considered, but suggestion is surely more likely to play a part in satiety, which one must agree is a relative term almost entirely. Hens, however, are very susceptible to hypnotic influences.

The evidence available shows that wild creatures display a greater desire for food during starvation, as compared with man and domesticated animals, and this is hardly likely to mean that training is able to abolish so primitive a phenomenon as hunger but points more to the probability that, as animals develop other interests and a greater mastery over their emotions, the effects of hunger show a modification. For instance, where a tiger would exhibit the greatest ferocity at being starved, man might face the situation with resignation and philosophic calm.

Referring to the inhibition of hunger during the spawning season, which probably underlies their (salmon) abstinence from food, it is significant that this circumstance occurs when sexual excitement is high and the result is probably indicative of a central factor in the suppression of the urge at a time when another fundamental urge is predominant. The lover's loss of desire for food can be similarly explained.

Another point of interest is the case of the hibernating animal. It is known that the temperature of the animal may fall to as low as 2° above freezing point and this produces a state of torpor or coma associated with paraplegia. (Pembrey) Under such altered conditions the brain is either unable to appreciate visceral manifestations (indicating a hungry state of the tissues) owing to its inexcitability or else the connections of the food centre are so disturbed as to abolish its functional activity. Probably starvation is to be accounted for on these lines in the hibernating animal.

A further point of interest arises in connection

with abstinence from eating, namely that where it is complete, discomfort is not marked (after the initial period) although if only partial, distress may be acute and may produce markedly degrading effects on conduct. H. Weber attributes the latter results to a failure of the pleasurable act of taking food to satisfy the appetite which is aroused but is not attended by an adequate supply of food substances. In other words the fundamental urge of hunger is virtually stimulated or teased only to be finally disappointed and the fruitless production of appetite adds to the torment of starvation.

However, when starvation is complete "the association of the realisation of the impossibility of obtaining satisfaction with emotional paralysis, implies, in addition, the presence of marked repression of important instinctual components".

Pavlov shows that the reflex of purpose may be weakened and even suppressed by a reverse mechanism and illustrates this by pointing out that after a few days of starvation the hunger urge becomes much weaker and in continued under-nutrition the instinct of living fails, which accounts for the indifference of the wasted and poorer classes to death.

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Chapter IX.

THE NERVOUS CONTROL OF HUNGER.

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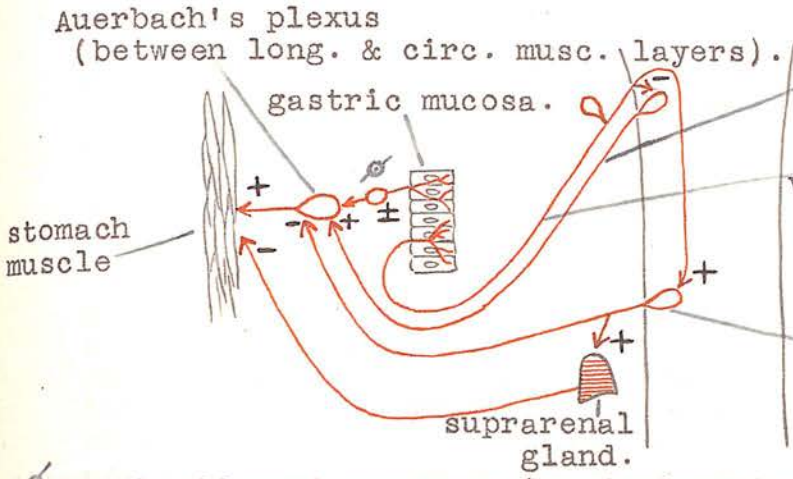
The theory that gastric empty contractions arise as the result of motor vagus impulses in response to stimulation of the motor vagi nuclei by central influences can be discarded at once, since division of the vagi does not interfere with gastric motility. The so-called gastric hunger contractions are due to an inherent automatic mechanism in the stomach wall, just as cardiac contractions are locally initiated, although modifications of that activity may be effected via vagal impulses. Keith described the presence in Auerbach's plexus of"nodal tissue" similar to that in the heart, and regards this as initiating gastro-intestinal motility.

The importance of impulses via the vagi producing " psychic" secretion of gastric juice concerns appetite only. The view that afferent stimuli via gastric nerves produce hunger and evoke conscious or subconscious reflexes must be studied and consideration must be given to the presence of a group of foci in the bulb, mid-brain, and cerebrum related to afferent and efferent conduction of stimuli and associated with reflex control of the gastric hunger mechanism. Finally the question of automatic or reflex processes in the gastric hunger mechanism apart from any central control is to be discussed.

Cerebral influences may be considered by studying the effect of decerebration in animals - the general results show either no change or an increase in the empty motility of the stomach. Decerebrated pigeons show restlessness when the crop is empty but rest when fed, and the period of quiescence varies with the amount of food ingested (Carlson). These results were confirmed by Rogers. Carlson also shows that the extirpation of the thalamus produces a disappearance of the conduct associated with lack of food in the above birds and this will be referred to below.

Luckhardt has shown that during sleep the empty stomach motility in man is either unaffected or increased, a fact which he attributed to removal of inhibitory extero- or entero- ceptive influences which normally occur in waking life. Carlson points out that the gastric motor mechanism is thus the only muscular (plain or striped) organ which does not show a decrease of tone during sleep and H.Weber attempts to explain this apparent physiological anomaly by psychological means. She points out that in sleep un-conscious activities are increased to the detriment of

DIAGRAM representing local and long reflex mechanisms involved in the inhibition of the gastric tonus and the hunger contractions from stimulation of gastric mucosa.



Tonus or motor neurones to stomach via vagi.

Afferent neurones in vagi from gastric mucosa.

\+ = Stimulation.

— = Inhibition.

Neurones in splanchnic nerves.

Local efferent neurones (predominantly inhibitory) from gastric mucosa to Auerbach's plexus.

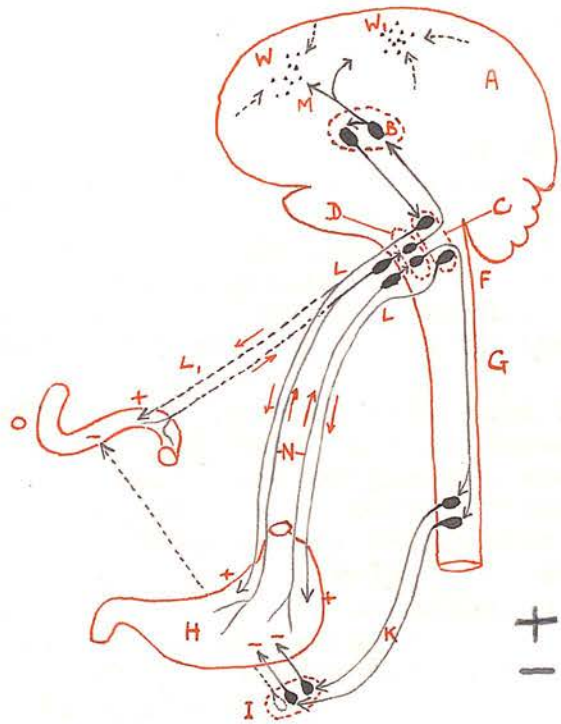


DIAGRAM
of the
NERVOUS MECHANISM
of the
HUNGER SENSE.

\+ = motor effects.

— = inhibitory effects.

A. Cerebrum.
B. Optic thalami.
C. Motor nuclei of vagi.
D. Sensory " " " .
F. Bulb
G. Spinal cord.
H. Stomach.
I. Visceral sympathetic ganglia.
K. Splanchnic nerves.
L. Motor fibre to stomach.
L_1. motor fibres to gut.
M. Sensory paths (Hunger) to cerebrum (hypothetical)
N. Sensory fibres from stomach. (in vagi).
O. Small intestine.
W. Cortical hunger centres.
→ direction of nervous conduction.

the conscious and as has been stated she regards hunger as being related to the unconscious. Moreover, this investigator suggests that the motility would result from vagal stimulation with sympathetic depression and it is our experience that splanchnic stimulation is associated with mental activity. The unique position which the stomach occupies amongst the neuro-muscular apparatus, in the above respect, is thus of exceptional interest although it is obvious that the stomach experiences during the night the longest period without repletion of its contents.

The effect of certain cerebral processes, where emotion is concerned, on the empty motility of the stomach as has been indicated, is usually in the direction of a depression, by means of splanchnic stimulation, but intellectual processes do not appear to affect the gastric hunger mechanism. It is to be expected,however, that the appreciation of hunger pangs in consciousness and the discomfort arising in relation to lack of food are subject to modification through psychic influences. This point was brought out by Carlson, for instance, when during starvation an appetising meal was shown to him;this increased the severity of the hunger pangs although the manometric tracings failed to show a corresponding amplitude of the gastric contractions.

It has been a matter of interest that hunger motility is not under direct central control, and vagal stimuli only influence gastric secretory activity as the result of psychic influences (appetite secretion),the resulting secretion producing quiescence of the stomach by acid inhibition. In other words, the influences via nervous paths are almost wholly in the way of inhibition.

Again, the psychic influence is evident when the question of bulk of food is considered in connection with satiety, for those people who are accustomed to bulky carbohydrate meals complain that they are still starving when given a meal of greater caloric value but of less volume. It is likely that craving for food is largely a matter of habit normally, since in civilised communities hunger is actually seldom experienced and satiety is probably influenced by self-deception under ordinary circumstances.

It must be recognised that contraction periods of the empty stomach are definitely influenced by the nature of the food ingested by the individual. Food rich in protein and fat is known to produce quiescence in the stomach for relatively long periods so that the onset of hunger motility is unduly delayed; Christensen has shown the effect of an egg-milk mixture in the stomach in this direction.

If only one meal is taken instead of the normal three meals a day more will be eaten during that meal than in an ordinary meal and so the onset of hunger will be retarded whilst the hunger motility of the stomach will either be correspondingly delayed or possibly when it does occur it may at first fail to give rise to sensations associated with hunger. That a change in the periodicity of feeding is important to preserve the food reflex applies especially in a child for when food or sweets are given between or before meals this tends to weaken or abolish the urge of hunger.

The necessity of attention on the part of the individual has been emphasised if empty motility of the stomach is to be recognised in consciousness, but as regards the hunger associated with tissue-depletion it is necessary to exercise considerable will-power in order to suppress the feeling of distress resulting from it. Pavlov maintains that the food reflex is stronger than the defensive reflex, within certain limits, and illustrates this point by the following experiment. With two external agents, namely food placed in a dog's mouth and electrical stimulation of the skin elsewhere, food and defensive reflexes were produced which induced a conflict in the central nervous system. As the electrical stimulation provoked a food reaction it is clear that the appeal of the nutritive agent won. Where, however, the stimulation involved bone, the urge of nutrition gave way to a defensive mechanism and a conditioned reflex was not evoked in respect of food by the electrical stimulus. The author regards hunger, in the fight for existence, as being of secondary importance when life itself is endangered, although one might add that often consequences are ignored in an attempt to obtain food if the urge is particularly powerful.

H. Weber in discussing the psychological factors in starvation indicates that the eagerness for food before puberty may be replaced by an opposite tendency after its onset and attributes this to a partial displacement of unconscious factors, connected with the instinct of self-preservation, by those connected with the race-preservation, whilst the greed of old age may be an indication of similar unconscious processes acting in the reverse direction. Carlson agrees that in old age gastric hunger contractions tend to diminish in intensity but the eagerness for food may increase - a condition occasionally seen in men of advanced years. These facts tend to show that there is no parallel between the hunger sensation and gastric motility as Carlson emphasises elsewhere in his work.

The influence of the mid-brain and medullary centres on gastric hunger motility may be studied by division of the vagi and splanchnic nerves and considering

the resultant changes. This procedure, however, obliterates cerebral influences and interferes with the paths of the long gastric reflex.

Double splanchnicotomy tends in dogs to increase gastric motor activity but this change is not of marked degree and periodicity is not abolished. Influences via the blood and vagi continue as before although psychic, reflex, and emotional stimulation are impaired as compared with the normal.

Factors associated with appetite are found to leave the gastric hunger motility unaffected. These results indicate that the apparent augmentation of hunger pangs in man, in the presence of sight, smell, taste of food, must rest on a central process of "facilitation".

Double vagotomy tends to produce hypotonicity of the empty stomach and some impairment of periodicity but psychic or reflex inhibition of hunger motility in the stomach is not greatly affected (slight diminution) and splanchnic influences are not found to increase proportionately in consequence of this operation.

Division of both vagi and splanchnic nerves, although productive of a permanent hypotonicity of stomach with an expected greater amplitude of hunger contractions, has no effect on periodicity although the intervals of relative rest may be prolonged somewhat.

These experiments prove the primary automatic nature of gastric empty motility and indicate that nervous factors play a purely regulatory role, this being further shown by the fact that an isolated stomach functions precisely as does the isolated heart.

Inhibition of gastric hunger motility may result from stimulation of the gustatory nerve-endings by various substances, varying with the intensity of the hunger contractions and with the strength of the stimulus, and if the latter is weak and its action is prolonged the stomach may escape gradually from this inhibition. A similar inhibition may be produced by chewing indifferent substances (from mechanical stimulation of the receptor nerves in the mouth) or again, by chewing palatable foods.

The observations of Boldirev who showed that hunger motility subsided when "spontaneous" gastric secretion occurred, or the "psychic" secretion described by Pavlov, may account for the cessation of motor activity of the stomach in the above experiments through the mechanism of acid stimulation of the gastric mucosa but as psychic secretion takes 2 or 3 minutes to develop whereas inhibition is practically immediate the mechanism is more likely to

be via a reflex direct from mouth to stomach, and this is supported by the fact that the inhibition disappears when the stimulus is removed from the mouth.

A minimal amount of gastric juice must be present in the stomach before acid inhibition ensues and Christensen has shown that if gastric secretion is of sufficient amount, following histamine injection, quiescence will occur in a fasting stomach although the state of the stomach activity at the time of the injection determines the time at which the inhibition response occurs. This observer was able to remove 192 c.c. of gastric juice from such a quiescent stomach and furthermore obtained relative rest in a fasting motile stomach by the introduction of 200 c.c. of water; he adds that other observers by 'mock' feeding in dogs were able to produce sufficient gastric secretion to effect quiescence, the duration of the latter depending on the amount of the secretion produced. In other words, quiescence results by inducing, by any means, a sufficient gastric content, in precisely the same way as ingestion of food effects an arrest of motility.

It is clear that psychic secretion may produce reflex inhibition of the fasting motility which merges into acid inhibition from a local gastric reflex. The act of swallowing may produce inhibition, just as the passage of a stomach tube may have this effect, by means of a "receptive relaxation" of the stomach (Langley) - this persists for 10 seconds. The reflex inhibition in the above-described experiment is not seen in lower animals.

The question of the effect of stimulating the stomach mucosa on fasting motility requires to be considered since hunger sensations, or sensations associated with hunger; result from stimulation of receptor nerves in the stomach by the empty contractions.

Hunger persists even when the stomach is completely excised, as we have seen, and complete isolation of the stomach from the central nervous system does not materially affect hunger motility.

Deficiency of gastric content certainly appears to favour motor stomach activity, although carbon dioxide secreted into the stomach or re-gurgitated intestinal juice (especially bile, which facilitates intestinal movements) may be factors in the initiation of the activity.

We have seen that "hungry" blood possesses the power to activate the stomach either by means of defective nutrient substances (especially sugar), or metabolites, or endocrine substances e.g. insulin and thyroid, which are known to influence hunger motility - but the stomach must be very sensitive to such influences since blood is, on the whole, very constant in composition.

Even minute changes have not yet been shown by chemical methods in the blood of hungry subjects although acidosis may occur terminally in starvation.

Bulatao and Carlson have shown that a reduction of 25% in the normal blood-sugar concentration is followed by an increase in hunger contractions and this hypoglycaemic condition may be produced by insulin presumably. This increase may be abolished by raising the blood sugar to normal again.

A consideration of these facts shows that although subject to extrinsic and local influences the empty motility (Leer contractionen) is an inherent property of stomach-muscle and the periodicity of motor activity may be aptly compared to that of other viscera e.g. the heart and uterus, which exhibit a like relative independence from purely nervous influences although adjusting their activity to physiological requirements.

Carlson has shown that ice-cold water has an inhibitory action on hunger contractions, varying inversely as the strength of the latter - the inhibition lasts for 3 - 5 minutes. It has been suggested that its action is by stimulation of the protopathic nerve-fibres, and when given as a drink the hunger sensation is said to be increased.

Acids in the stomach produce inhibition of motor "empty" activity when introduced directly (via tube or fistula) and the quiescent interval varies in duration with the amount and acidity of the fluid introduced; the period of relative rest is obviously altered by the neutralisation of the acid (by regurgitation of intestinal juices, or by the action of the mucus in the stomach) and by the passing of the acid out of the stomach. The acid must be of a minimal concentration to produce inhibition. The work of Hoelzel and Kleitman suggests that in protein starvation the acid gastric juice acts on the duodenum and produces an element of hunger sensation - water may act so, injected via a duodenal tube, and in this form of starvation a hypersensibility of the alimentary mucosa is shown, along with a respiratory increase. Their investigations suggest that hunger sensations may have arisen from duodenal motility (associated with regurgitation into the stomach) in the presence of a high acidity and fat in the stomach.

Chapter X

THE CHEMICAL CONTROL OF HUNGER.

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Unquestionably, chemical factors play an important role both with regard to the control of hunger and in modifying fasting motility of the stomach and intestine.

Bardier was of the opinion that in the hunger state the blood and tissues possessed hungry properties which stimulated a theoretical hunger centre.

The observations of Tschkitscheff that the blood of an animal during digestion diminishes, on injection, the hunger contractions of another animal, and the injection of blood from a starving dog when its stomach is quiescent increases the stomach motility of the recipient, whereas if the donor's stomach is active the injection inhibits the activity of the resipient's stomach. This suggests a hormone control of hunger contractions and indicates pressor and depressor elements in its constitution (Biedl). Tschkitscheff investigated the question of the modification of hunger contractions by every factor which influences the blood via the alimentary canal. He showed secretin to possess such an action and also found that the products of gastric and pancreatic proteolytic digestion in vitrio gave positive results although various amino-acids (leucin, alanin, tyrosin, and aspartic acid) gave negative results. Thus the end-products of proteolytic digestion modify hunger contractions, and Bulatao and Carlson have shown that an inhibition of hunger contractions result from glucose injections, and an increase with insulin injections.

Luckhardt and Carlson first noted that the blood of starved or diabetic dogs increased gastric motor activity of normal dogs and showed that phloridzin glycosuria in dogs increased the gastric empty motility. Templeton and Quigley have advanced a theory which indicates that the presence of glucose in the duodenum gives rise to a hormone which inhibits hunger contractions.

They further show that duodenal motility may result from insulin injections and which may occur apart from, or may precede the gastric response, so that it may be associated with the causation of hunger. These investigators hold that only large doses of glucose and insulin affect hunger contractions and so are more inclined to the hormone theory.

Ivy and Fauley quote Yesko's experiment of pancreatectomy in producing a decreased emptying time of the stomach with polyphagia and have obtained such results by ligation of the pancreatic ducts. They allude to Lorenzi's work also in which he showed that feeding with thyroid extract shortens the emptying time of the stomach by 2¼ hours as compared with the normal. Haudek and Stigler stated that the stomach empties more rapidly with hunger than without.

Cannon and Washburn showed a greater tonus of the stomach in hunger and that it increases proportionately as starvation continued. Ivy and Fauley have further shown that hunger and fasting, up to 72 hours, produces a decreased emptying time of the stomach and point out that thereafter this is less marked because the tone of the stomach goes and inhibitory factors e.g. nausea, weakness etc. set in, probably by splanchnic stimulation as the result of emotional disturbances.

Perusse and Rozen emphasised the fact that increased heat-production must be met by increasing food ingestion to spare the body tissues, which carbohydrate does particularly well.

They show that the blood of starved animals, exhausted of nutrient materials, may contain metabolites which act both on specific receptor cells (the threshold of irritability of which is lowered by a lack of nutrient substances) in the stomach giving rise to hunger contractions, and on the brain producing the hunger sensation, but agree that hunger contractions and the hunger sensation are not always parallel.

The failure of the hunger sensation to appear in the presence of powerful hunger contractions may be attributed to the toxic effect of metabolites on the central nervous system and nausea is experienced instead. If, however, the metabolites stimulate the stomach and not the central nervous system, hunger contractions may be interpreted as pain (hunger pangs).

The above authors point out that hunger contractions are inhibited when food is taken and theoretically the hunger sense should also disappear, which is not so, so that hunger contractions do not presumably produce the hunger sensations. The nodal tissue which Keith describes in the muscular wall, initiates the motility of the stomach, which is essentially automatic, and so since the stomach exhibits periodic activity when starvation is not actually present it is doubtful whether metabolites play a significant part in the ordinary stomach motility, in association with its empty state.

Rozen and Perussé have produced inhibition of the hunger contractions by giving magnesium salts per os

which can be relieved by the administration of calcium salts although the latter have no effect ordinarily on hunger contractions. When given by injection the central effects of these salts mask the above results.

The above findings indicate how blood changes influence gastric hunger motility and this leads one to the conclusion that in starvation and altered metabolic conditions, chemical as well as motile visceral factors determine the hunger sensation.

Such chemical factors may act on the stomach muscle itself and on the hunger centres (vagus motor, thalamic or cortical) they may increase the tonus of the stomach in hunger, induce independent hunger contractions, or determine the periodicity of fasting motility. Hunger contractions may only be interpreted as hunger pangs, possibly, in the presence of chemical bodies in the blood of the hungry organism.

It has to be seen whether chemical factors in the blood can depress the hunger motility - this depression occurs very readily in connection with mechanical and chemical stimulation of the stomach mucosa as we have seen.

The function of this latter depression which is associated normally with the presence of food in the stomach must not be confused with the transient relaxation immediately following food;the former only arises as digestion proceeds and as the nutrient products in the blood increase.

Consideration has already been given to a pre-digestive phase in hunger which Mulinos showed in dogs and the essential points of his observations may be recapitulated here. The immediate inhibition of the stomach following ingestion of food (a reflex relaxation from the mouth and gullet) is followed by a motile phase which only occurs when food is taken and which is shown by an imcrease of the tone and contractions of the stomach. This active phase is followed by a fall in tone and activity after $\frac{1}{2}$ - I hour which marks the onset of the digestive phase. The fact that this predigestive phase occurs only with food (e.g. meat or moistened bread etc) indicates that possibly a chemical factor related to the food enters into the process since it does not arise when indigestible substances are taken.

50% glucose solution via a gastric fistula was shown to depress hunger activity without its subsequent augmentation. It is of interest to note that the predigestive activity of the stomach resembles gastric motility following insulin adminstration. The latter injection produces I hour later a tetanic of contraction unaffected by food(as is the predigestive phase) but destroyed by intravenous glucose although the latter does not affect the hunger or after -feeding curves.

The predigestive phase may be due to a non-specific chemical stimulus and can be abolished by the injection of atropine. The stimulus however if not a chemical one is certainly not a psychic influence since food introduced through the stomach tube or via a gastric fistula may produce this after-feeding motile effect in the stomach.

This predigestive phase is not a continuation of the activity inhibited by the taking of food but is a new type of activity and is unaffected by taking more food. Its function is presumably to prevent the inhibition following inadequate food intake resulting in a sense of satiation as this would produce intime under-nutrition.

Although the injection of 1c.c.of 20% NaCl solution as Hughson and Scarff showed causes a rise in the Cl-ion of blood and increases gastro-intestinal motility similar to the predigestive activity it is not clear whether this latter phase is so produced.

Mulinos shows that the gastric response to insulin hypoglycaemia by hypermotility is dependent upon the presence in the diet of some factor containing Vitamin B.
Burack and Cowgill show that the loss of the urge to eat in dogs results from lack of Vit B1 or some other substance (not Vit B2) since tiki - tiki (a material practically devoid of heat stable Vit B2) relieves the condition.
Graham and Griffith suggest that both Vit B1 and another factor present in autoclaved liver (rich in Vit B2) are necessary to prevent anorexia. This vitamin deficiency probably acts via the vagus nerves.

Intravenous insulin has been shown by Mulinos and others to depress stomach motility initially although in 5 - 30 minutes gastric hyperactivity of the hyperglycaemic type results.

Christensen's contribution to the subject from the chemical aspect may be summarised as follows viz., a minimal gastric content is necessary to produce relative rest of the stomach whilst he has shown that fats and proteins, by their depressing effect on gastric motility by the products of fat digestion or by their greater stimulation of the acid gastric secretion respectively, tend to remain longer in the stomach than carbohydrates and cause a correspondingly more prolonged inhibition of motor activity.

Carlson has studied the effects of haemorrhage on hunger and hunger motility in dogs and shows that if the bleeding is severe marked hunger is produced with increase of hunger contractions, these effects being due to the possible removal of nutrient substances from the circulation. Its action is evident for 24 hours but obviously if loss of blood is extreme the general condition of the individual complicates the results.

Cocaine and arsenic are habitually taken by certain peoples with the view to allaying the sense of hunger and the action of these drugs is probably wholly confined to the cortex. The action of nicotine has been dealt with in another chapter.
Morphine produces a profound inhibition of both hunger contractions and hunger sensations in common with its general depressant action on all vital processes.
Histamine depresses hunger motility at the same time stimulating the secretion of gastric juice and the latter may determine the former effect.

Full consideration of all the drugs which produce motor or secretory effects in the stomach would serve no useful purpose but a general statement may be made that drugs which stimulate the stomach musculature either via the vagus nerve-endings or by direct action on the muscle fibres tend to augment the fasting motility; those substances which produce relaxation of plain muscle or which cause splanchnic stimulation or in any way induce an output of adrenaline cause a corresponding diminution in the hunger gastric motility.

It can be seen that the gastric hunger mechanism is very susceptible to depressing and stimulating influences although as we have seen it is essentially automatic in nature. Its various responses are correlated with the needs of the organism and its activity appears to be determined in part by the very substances with which it is ultimately concerned. All the facts point to the conclusion thatthe blood - changes reflect accurately the needs of the organism for the various food factors essential to maintain life and health and probably the centres in the central nervous system controlling nutrition receive the signals of distress due to lack of nutriment through the medium of the circulating blood.

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Chapter XI

PAVLOV'S "FOOD CENTRE".

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Pavlov's researches require separate consideration since his work has opened up entirely new avenues in the realm of nervous phenomena.

This great physiologist believes that there is a centre (or centres) in the central nervous system which controls the activity of the animal in regard to nutrition in precisely the same way as the respiratory centre governs respiration.

This centre directs the organism in acquiring food from outside and in ingesting it and at the same time activates the salivary and gastric secretory mechanisms along with such skeletal muscles as operate in relation to intake of nutriment.

Pavlov chooses to use secretory, as opposed to muscular, activity, as evidence of the functioning of the "food centre" since the former indicates more accurately its activity, being wholly related to the question of food, whereas the voluntary muscles involved may subserve other functions.

He maintains that the food centre is stimulated by the chemical composition of the blood of the animal which has not fed for some hours and believes that such blood develops "hungry" properties. This stimulation then expresses itself on the part of the animal by a motion directed towards obtaining food by a secretory activity, forthwith, of the upper digestive tract. This, he shows, is analogous to the mechanism of respiration.

Pavlov shows that every centre can be stimulated either automatically or by means of entero-ceptive and other impulses, and points out that, so far, no single reflex stimulus has been shown unequivocally to be absolutely necessary to initiate activity of the food centre.

The vagi, splanchnic and gustatory nerves have been divided without producing any apparent difference in the health or in the desire (urge) for food. This favours the view that it is the chemical condition of the blood which decides the activity of the food centre, and whereas, at first, the stimulation is latent, later it gives rise to a movement reaction towards food and the other phenomena associated with its ingestion and digestion.

In order to demonstrate the activity of the food centre a salivary conditioned reflex is established by means of flashing a light before acid is introduced into a dog's mouth (which latter chemical stimulus per se produces salivation) and after repeated association of these stimuli salivation will eventually result from a flash of light alone. A delayed conditioned reflex may be produced by not introducing the acid until 3 minutes have elapsed after the flash of light - in such a case salivation will not occur until the 3rd. minute (just prior to the introduction of the acid). This delay of salivation (salivary reflex) is due to internal inhibition of the action of bright light and the inhibition itself may be inhibited through the medium of any usual normal external stimulus acting during the interval between the flash of light and the introduction of the acid, as shown by the appearance of salivation. The fact that latent stimulation of the food centre acted on the "acid reflex" centre was shown by the following events. In a dog usually fed at 5 p.m., the experiments resulting in a delayed salivary reflex (above mentioned) were positive at 10 a.m., but between 3 and 4 p.m. the salivary reflex failed to show delay (escape of inhibition).
The different centres are interrelated and one can inhibit another. The "acid" centre is inhibited in the case of a delayed salivary reflex but the increasing latent excitation of the food centre produces a paralysis of this inhibition, as do unusual external stimuli, and immediate salivation results. The latent excitation of the food centre must depend upon the fact that the stimulation is inadequate to produce response owing to the intervention of internal inhibition. This is shown objectively in a dog who exhibited no activity of the food centre, who, when acid was placed into its mouth, showed an "acid" motor reaction- which, when completed, was followed by a marked "food" motor reaction; the latter activity resulted if any object were near which was associated with feeding (i.e. a conditioned reflex). Thus a positive expression of the food centre activity was determined since its inhibited state was inhibited by the reciprocal action of centres (e.g. the excited acid centre) namely, a dis-inhibition of the centre was postulated. Decerebration operations tend to weaken the inhibition. A normal starved dog when given meat powder exhibited salivation which was followed by an excitable state, which in turn passed off in about 5 minutes along with the cessation of salivation. A dog whose posterior cerebral hemispheres were removed was quiescent if not fed but when food was given marked salivation and excitability resulted which persisted for as long as 1½ hours. Salivation exhibited irregular rhythmic variations (a phenomenon indicative of a conflict of antagonistic processes - activity and inhibition.) and was, in the above experiment, taken to indicate that the

food centre when in a state of latent excitation contained an inhibitory factor also.

Pavlov shows that the activity of the food centre not only activates the organism and digestive secretion but also produces sensations of appetite and hunger although the former sensation cannot be proved in animals but only inferred from objective manifestations. The interesting point that anorexia in man is remedied not by nutritive but by unpleasnt subs. (bitter tonics) is analogous to the stimulation of the food reflex by acid stimulation in the dog and illustrates the fact that the activity of the food centre may be aroused by this disinhibition. It is obvious that section of both vagi, although not affecting the fundamental gastro-intestinal activity. removes the important afferent path to the receptor nucleus and so abolishes reflex stimuli to the food centre.

A natural conditioned reflex for food was tried in a dog - the sight and smell of food for half a minute gave three-five drops of saliva. When fed the dog then exhibited a period of excitability for food (sniffed, licked, and pranced about) and if, when quiescence returned, the same conditioned reflex was tried, 10-15 drops of saliva were secreted, an increase due to the increased activity of the food centre by a peripheral reflex through feeding the animal.

The circumstance is seen in every day life for if, when we have no desire to eat, a small amount of food is taken the gustatory stimulation produces appetite and the urge for feeding is established. The augmented activity of the food centre implied by the increased salivary yield was attributed to the combined reflex stimulation from the mouth and stomach, but Pavlov found that when repeatedly applied the same conditioned reflex produced a decreased amount of saliva on each occasion until finally no response occurred.
This failure must have arisen from inhibition of the activity of the food centre by influences from the stomach as the result of contact of food or in association with the early stages of gastric secretion, and when the results of Mulinos in reference to the pre-digestive phase of stomach activity is considered these conclusions are manifestly of the greatest significance.
The facts indicate that the activity of the food centre ceases until digestive processes are over, and the means whereby this inhibition is effected has been shown to be due to gastric reflexes by Boldirev, who failed to observe any inhibition of, or alteration in (after frequent repetitions), the conditioned reflex when "mock" feeding in dogs with oesophageal fistulae was undertaken; i.e. the flow of saliva remained quantitatively the same when food did not enter the stomach.

Pavlov mentions the fact that when paroxysms of good appetite are felt (obviously he treats 'appetite' and 'hunger' here as one manifestation associated with food) they are accentuated by a small amount of food but disappear completely in 5-10 minutes and again the relation of this observation to the findings of Mulinos is to be noted, when he states that if, in hunger, inadequate amounts of food are taken there occurs a loss of desire for food if an interval is allowed to elapse before more food is taken.

The inhibition of hunger motility by food on this assumption merely indicates its relation to digestive activity since the hunger sensation soon returns if there is a marked depletion of food-substances in the organism.

When we refer to the cessation of repiration produced by voluntary over-ventilation of the lungs (forced apnoea) it is seen how closely related the food reflex is to the respiratory reflex and such an analogy indicates the essential nervous origin of processes related to food ingestion. The influence it exerts on chemical equilibrium in the body, as well as the effects of the latter upon it, seem clearly established.

That the activity of the food centre is highly complex can be seen but it involves essentially a reflex arc, the actual centre, or centres, being the central part of the arc and in the nature of receptor (sensory) stations, subject to numerous influences both nervous and chemical. This brilliant conception of the food centre by Pavlov indicates that the afferent path of the reflex arc is purely executive, in so far as the muscular response is concerned, since the same muscles related to a movement reaction towards food may be used for numerous other purposes.

The afferent paths to the food centre are legion but although such a variety of stimulations reach the centre via the former tracts, relatively stereotyped effects result e.g. salivation etc. It is the function of the food centre to initiate muscular movements in response to many stimuli associated with food and other related factors.

The situation of the food centre may be suggested from the effect of decerebration of pigeons, who, although exhibiting hunger phenomena (restlessness etc.), are quite unable to nourish themselves in the presence of plenty, although they are immediately set at rest by putting grain into their mouths and do not exhibit a return of muscular activity until 5-7 hours have elapsed.

It is clear that although the simpler processes connected with feeding arise from the activity of centres below the cerebrum, the main food centre consists of scattered collections of neurons in the cerebral hemispheres.

Chapter XII

THE TWO COMPONENT THEORY OF HUNGER.

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D. Katz, the originator of this theory, holds the opinion that the hunger instinct is stronger than the love instinct and shows that hunger in its broadest sense is dynamic and not static. Nothing can arouse us as hunger does since it leads us to a realisation of our existence. The consciousness of one's environment is not something purely passive but is based on creative acts on the part of the possessor of this consciousness. Hunger, in mobilising the muscular system, leads to motion on the part of the organism, although this factor is less prominent in adults than in children and animals.

Hunger, moreover, makes men reckless and enables them to overcome obstacles and although this probably acts through a stimulation to action from necessity yet Noltenius has come to the conclusion, based on his experiences on war service, efforts in sport and particularly on severe exertions in tropical climates, that, after mastering the initial period in fasting, there occurs a sensation of increased performance ability which leads also to an effortless conquest of difficulties. He also noted in addition to these bodily phenomena a euphoria, which however was not the cause of the change. In his opinion the action of hunger, in the above sense, is by giving the body an opportunity by diminished food intake, to reduce the water content and especially to eliminate the various accumulated waste-products so that muscle-work may be raised. This hunger-treatment should not be exaggerated since then harm instead of benefit results .

The stimulating effect of fasting among certain religious peoples can thus be attributed to the increased nervous excitability of the organism in the absence of food and to the rest afforded the digestive organs in particular and the metabolism in general.

Individual differences in food intake appear as the animal grows up - for instance, the infant takes only milk at first and similarly birds commence by eating flesh and later on vegetables. Thus, as experience with various substances and appetite develop the more recently acquired materials seem essential in order to appease hunger. In captivity however, man and animals exhibit a certain measure of adaptability as regards food requirements. It is true of all animals that the greater the hunger, the less particular they are as regards the taste and nourishing properties

of the food and in extreme cases they devour thoroughly indigestible materials. During the Great War the Germans made use of tree bark as an ingredient in their bread, this probably acting also by increasing the bulk of ingested substances so as to give a sense of fullness in the stomach and apparent satiety.
Animals and birds show a regular rhythm in their need for food, eating most in the autumn and least in spring. Similarly a young baby feels hungry at precisely the same hours every day.
It is certain that man is easier to please when satieted, as the saying that "the quickest way to a man's heart is through his stomach" implies.

The two component theory of hunger postulates the dependence of hunger upon two factors:- (i) the psychological and physiological condition of the subject, (ii) certain external factors e.g. the amount of food available, the impetus given to eat by the presence of another person eating etc. Experiments with a hungry hen have proved that it will eat more if placed before a large heap of corn than a small heap. A hungry hen which has eaten its fill will restart eating if joined by another hen which is hungry. The latter fact may be compared to a phenomenon in camels, relating to the ingestion of water. The Bedouin Arabs in order to induce their camels to drink to absolute capacity before a journey across the desert, first of all allow these camels to drink their fill and then find that by bringing thirsty camels near to drink, the former, apparently filled, animals will re-commence drinking, and a further ingestion of fluid can also be produced by exciting the camels by means of music, dances etc. This is of interest because the question of appetite does not arise in the case of ingestion of water and so the fact that hens, apparently satiated, may be induced to take further nourishment probably involves factors other then appetite.

The observation of H. Weber that "the mood of the moment , the society, and the surroundings generally must be to some extent taken into account (as regards appetite) shows the ultimate instinctive basis upon which each rests", and it is probable that the influence of these factors mentioned may apply equally in the case of hunger. The truth of the saying "Better is a dinner of herbs where love is, than a stalled ox and hatred therewith" cannot be disputed and although this applies partly to the question of appetite, doubtless emotional factors may produce a profound effect on such an instinctive urge as hunger. Katz points out the beneficial results of cutting down the quantity of food taken at meal times, proving this by experiments in dieting and noting that he always felt in better condition after cutting down his meals.

Presumably this writer, by eating in response to hunger without allowing appetite to act as an indication of the quantity of nutriment required, restricted his diet more nearly to his physiological needs.

It is a well known fact that considerable will-power is required to reduce one's weight a certain number of lbs (without the use of drugs or medicine) simply by refraining from eating at meal times up to the point of satiation.

Hunger and satiety are correlated but the latter in contra-distinction to the former is a relative and not an absolute term. For instance, the body may be satiated in respect of a certain food or drink but is still able to take in a considerable quantity of another dish. Herein lies the art of the chef serving the dishes in the correct sequence. The fonder we are of a dish the stronger does it repel us if we continue to take it beyond the point of satiation.

Rosa Katz deals with the question of psychology in the feeding of children and shows the value of auto-suggestion, in contrast to the use of patent foods and force, which should not be used, in the case of a temporary loss of desire for food. She relates that when the children were allowed to order what food they wanted on the strict understanding that if it were prepared by the mother it would really be eaten, they ate quite a healthy meal. The other method she adopted consisted in giving them perfect freedom to choose whatever they liked from the food on the table or in the larder; here we get such interesting and impossible combinations as fried potatoes and honey but they were eaten heartily and without any unpleasant consequences. These observations seem to show that there was little wrong with the appetite in these children but that they lacked the urge to eat under the conditions which obtained prior to these experiments. We are all familiar with the child who when at home habitually picks at its food although when dining together with other children, may eat the same food with great zest. It seems difficult to determine with certainty the cause of the failure to eat amongst these children, but, on the whole, one favours the view that there is a temporary loss of the urge to eat from some emotional disturbance whilst the appetite does not show a fundamental defect and is readily stimulated under suitable psychological conditions.

Bayer has continued research on the lines laid down by Katz. He points out that, to date, the physiological aspect of hunger has received a disproportionate amount of attention as compared with psychological consideration. He has endeavoured to show the importance of the animal psychological method of approaching the problem, and chose hens as the experimental animals because (as Katz suggested) the elementary psychological laws in them

makes them suitable subjects for study. In man, the problem of hunger is rendered extremely difficult because of the complexity of the psychic element.

The work of the Pavlov group is essentially physiological, although it is of great psychological interest; and the Carlson school of experiments stress the strength of the hunger urge compared with the force of other urges (sex and thirst).

Although the psycho-physiological mechanism of hunger, as emphasised by the physiologist, is of greatest importance, the two-component theory has shown that the kind and degree of taking nourishment depends not only on subjective psychological and physiological conditions, but also, to a certain degree, on hitherto hardly suspected external conditions (environment) in which the hungry organism finds itself.

Bayer has taken the greatest precautions in his experimental hens to standardise them to hunger - regular feeding, complete satiation, equal intervals without food, steps to preserve the hens in health by means of free exercise, water and fresh food (between the experimental days) various ages, cross-bred fowls - all these factors have been attended to in order to obtain results upon which dependence could be placed.

He, firstly, investigated the question of the fondness for various foods amongst hungry hens by comparing the amounts of various kinds of grain eaten on different days, when amounts in excess of what they could actually eat were given, and then he gave them a choice of two kinds of grain. It was found that they ate more of the grain for which they exhibited a preference, i.e. in order to produce spontaneous satiety more of the favourite food is necessary. When given a few grains of two kinds, one of which was their favourite, they ate up the latter first before eating the remainder. Even when hens are teased with grain when hungry, they eat the grain for which they show a preference rather than that which was shown them first.

Animals show temporary predilections for certain food on different occasions (appetite) within periods of natural feeding - for instance, omnivora may favour vegetables at one time, meat at another, and so on.

There is also a difference of predilections for food amongst animals e.g. carnivora, herbivora, and omnivora., i.e. basic urge for certain food is stationary.

Changes in preferences occur spontaneously from time to time, and the first choice and the last choice (when tests were made in hens to establish the order of preference) indicate whether most or least will be eaten in order to produce satiety. The intermediate preferences

especially show changes, although wheat, when a second choice, remains fairly constantly in that position even when repeated feedings are made with this grain in order to try and make the hen revolt against it. (This is of interest since although bread is not a first choice with man, he rarely grows tired of it). On the other hand, if repeated feedings of the first choice of grain are made, i.e. maize, the animal will revolt against it and when given a choice of grains, some other kind will be favoured first; moreover, superfluity of the favourite produces a lessened intake, subsequently, of other foods. This is seen in children of rich families who when they are plentifully supplied with their favourite dishes often show a decline in their desire for food.

To show the influence of external circumstances on food-intake, Bayer first attempted to indicate the importance of the background on which fodder was supplied to hens. He compared the amounts eaten from hard and from soft surfaces and found that more grain was eaten and more rapidly ingested from the soft surface; moreover, when a choice was given of the different surfaces, side by side, the hen would invariably choose the soft surface from which to eat the grain. Even after demolishing the grain from the soft surface, the hen, although obviously not satiated, would pick idly at the top of the heap on the hard surface and then return to the soft surface and peck at it; although it ate vigorously again when more grain was placed on the soft surface. The state of the hen was such that it still remained hungry after eating the small heap from the soft surface but was not hungry enough to eat from the hard surface, however. The reason for this was probably that the painful vibrations of the beak from its impact on the hard ground, in time, inhibited the urge to eat, just as Pavlov's dogs would continue to eat, when nocuous stimulation was applied; unless the latter was so intense as to threaten the dog's life. The question of the impact of the hen's beak on the hard surface suggested to Bayer that if he placed the grain on a plastic surface (putty) the hungry hen would leave impressions of its pecking and so determine whether the beak actually did strike the ground in feeding or merely closed about the grain. He found that the beak did strike the ground, and of greater interest still, that the depth of the impressions on the plastic surface varied with the intensity of hunger - in other words the energy in feeding was proportionate to the degree of hunger, and as satiety was approached the impressions grew fainter. This agrees with the increased excitability seen in higher animals in the hunger state.

The experiment with the soft and hard surfaces shows that whereas hunger indicates an urge for nourishment, the pain produced by eating from a hard surface tends

to inhibit the desire for food and so at some point equilibrium is reached, shown by failure of the hen to eat from a hard surface although it will continue to eat further amounts if offered grain on a soft surface. In time the memory of the discomfort of eating from a resistant surface will suffice to arrest any tendency to feed under such conditions - i.e. experience develops for that particular circumstance.

Bayer found that Katz was correct in stating that a hen would choose the larger of two heaps of grain from which to feed and would, if large and small heaps were presented on alternate days, eat 75% more in order to produce satiety when feeding from a large heap, even although the smaller heap contained more than sufficient for it. Thus, in equal physiological conditions of hunger, the lust to eat depends largely upon the amount of food offered in the experiments. Further, there is a greater avidity for eating from the larger heap as shown by a shorter time to reach satiation stage in this case.

These results, in the light of the physiology of hunger, are unexpected, for one would expect an equal physiological hunger state to express itself in the same way, as long as the opportunity was given to ingest sufficient food to satisfy one in the presence of more than adequate requirements.

In order to compare the amounts which hungry hens would eat, large and small grains of food were used (rice was chosen since the rice-grain and the rice meal conformed in all respects except as to size) and 150% more of the whole rice was required to produce satiation than the broken grain. This may possibly have been the result of the excessive drying up of the mouth juices by eating the smaller grains, but fatigue in feeding probably contributed a part, since more energy is required in eating smaller bites although they may be taken more quickly. These points show the importance of psychological factors in hunger.

When different kinds of food were mixed, Bayer found that, if a mixture of two grains of medium preference were given, more of the mixture is eaten than of each single kind (on test days), and more of the mixture will be eaten than of a single kind, even if the hen shows a preference for the latter. The increase required to produce satiety may amount to 34%. Theoretically, one would have expected the fowl to have selected the preferred grain, when a mixture which contained it was offered, but whilst, at first this was the case (as when small amounts of 2 kinds of grain (mixed) were given), yet after a certain degree of satiation was reached no discrimination was shown. It is a commonplace observation that a change of diet stimulates

the desire to eat, and it seems reasonable to assume that when conditions only allow of the same food to be taken with monotonous regularity, they tend to depress the very urge to exist, upon which the lust to eat ultimately rests. The combination of foods increases the urge to eat and a further increase is shown when a mixture of three foods is given. A limit is probably reached, however, when it becomes a physiological impossibility to ingest further amounts.

The effect of the order of feeding of different kinds of grain has been studied by the same observer who offered various kinds of grain in sequence and allowed the hens to become satieted with each variety before substituting another. By such excessive offering of grain a great increase in food intake may be effected, showing that satiation is only relative up to a point; if food is offered in the reverse order of preference, more is eaten than when the food is given in order of preference although an increased intake can be obtained by either procedure. This former procedure illustrates the habit amongst human beings of "keeping the best until the end". Every mother knows the disastrous effect of feeding a child with dainties between or before meals and the same scientific fact explains the secret of a great chef who chooses the order of food in such a way that there always remains the possibility of eating just one more dish.
It may be argued that these experiments show the effect not of hunger but of appetite on food intake, but it will be agreed that the external factors seem to involve something more fundamental than appetite in producing, by their suggestive stimulating value, some added urge (to ingest nourishment) more akin to greed than necessity.

By a process of re-presentation of food, suggestive methods of feeding are carried to a maximum. Hens are allowed to eat to satiation but before having a chance to become quiescent the residual grain is removed and thrown down before the bird again, who immediately re-commences eating - one hen restarted eating 15 times when the food was so re-moved and re-presented. Further exciting of the hen could be induced by offering grain, from the hand, closing and opening the latter, and whereas every hen responds to one kind (usually a favourite food), there is no response to some grain. It was shown that when the food moves the hen is excited to eat.

The common example of the dog who lies calmly beside a bone, and who, when one attempts to remove the bone, snarls and recommences its attack on the morsel, illustrates the same point. It does not seem to be the result of a stimulation of the appetite so much as that of the defensive urge, which, after all, as has been mentioned, forms one of the earliest means whereby nocuous substances previously regarded as having potential food-value, are rejected.

Bayer deals with the social influence of an animating or urging animal on food intake. It is known that the sight of an eating hen acts incitingly on other hens who come at once running, even when previously they showed no sign of hunger.

The presence of a hungry hen (the animating chicken A) eating, will induce a satiated hen (experimental chicken E) to restart eating. When two hens are put together the one develops into a despot and the other falls into an accepted subordinate position (a state of affairs by no means foreign to human relationships!) and so double-checked experiments in which the despot hen was also the experimental (E) hen, and the subordinate one the animating (A) hen, and vice-versa, were carried out to eliminate errors arising from the effects of inferiority or superiority on the part of a hen.

To produce a high degree of satiation the experiments were done with wheat, which stood high in order of preference. The hungry hen was placed before a large heap of wheat and could eat until satiated, and when another hungry animal was brought near to the sated hen (A) and started to eat, the former hen recommenced eating actively. If the satiated hen was a despot it attempted to prevent the hungry subordinate from eating by pecking at it (presumably from envy) but as this had little success with the hungry fowl, the satiated despot recommenced eating but did not omit to give occasional pecks at the hungry subordinate.

When the animating hen is the subordinate one it will also recommence eating when a hungry despot hen commences to eat and the latter, although so occupied with eating, still finds time to bestow an occasional peck on the satiated sobordinate, who makes no attempt to counter-attack. That a subordinate sated hen, will, despite its fear of the hungry despot, recommence eating shows the strong inciting influence of the act of eating, although the first named eats guardedly and somewhat surreptiously. When the animating animal is satiated no exciting influence then results on the experimental animal.

The experiments show that the advent of a starved voraciously eating animal amongst others, already satiated, set these latter off eating an additional 34% food. Why hens, already satiated, should restart eating may be due to imitation, but it is strange that this factor should affect eating in the full, as well as the empty stomach, even in the presence of fear of the despot, who exhibits envy towards the eating subordinate although fully satiated itself.

The social influence of 3 animating hens on eating in a sated hen is greater than that seen with one inciting animal - the increase then is 51%. Three fowls

produce a more powerful "mass suggestion" than does the "individual" suggestion of a single animal.

When one hungry hen is introduced amongst three satiated hens and commences to eat, the effect on the sated hens is very slight (10% increase on an average) - possibly this is to be explained by the fact that the three hens were fed communally and so had reacted one on the other in a stimulating way and so were not susceptible to further suggestive influences. Thus the behaviour of several sated animals on one hen is greater than that of a single one on many.

Communal, instead of individual, feeding of hens produces a 90% increase in food-intake.

Thus the subjective condition of the organism is one factor, but external circumstances play a more important role than is usually recognised.

Gallus Beck has made further contributions to the Two-Component Theory of hunger by studying the food intake of fowls under the influence of varying conditions of illumination and by varying the time-intervals of meals.

He found in his investigations that additional problems presented themselves, e.g. the dependence of food-intake on egg-laying, on moulting and on co-existent thirst.

In discussing the influence of physiological factors, egg laying has been found to produce a diminution of 30% in food-intake (as compared with that on a normal day) and the hen is observed to peck more slowly and deliberately, being readily disturbed in its eating by extraneous noises.

Water intake has been shown to influence ingestion of food. Whereas normally, fowls drink water at frequent intervals during the day and especially during meals, these hens have been noted to eat 40% more fodder than those which are allowed to drink water, up to, but not during eating. If water is withheld for some hours before giving food to a starving hen, then if food and water are presented together the hens will unhesitatingly, and in all cases, go first to the water for a prolonged drink, and then partake of 15% less food then normal birds given water before and after food. This observation shows that thirst is a biologically more powerful stimulus than hunger.

During moulting there is observed a gradual and often considerable loss of weight in fowls. Food intake, however, increases throughout the moulting period and remains high for some time after the normal weight is restored.

The effects of different illumination on food intake, have been shown, e.g. hens kept in the dark will eat much more slowly, and only half the normal quantity

of food, but if, after they have had their fill in darkness and have ceased to eat further, light is admitted they immediately recommence eating. The total amount thus eaten, in darkness and light, is always slightly more than in normal illumination only (15%). More food is eaten in red and yellow light than in ordinary daylight, whilst in green and blue light, less food is taken. It is known that the former colours have a stimulating effect on the organism whereas the latter colours have a sedative influence.

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SUMMARY

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A consideration of the foregoing facts and hypotheses concerning the nature of hunger indicates its complexity.

There can be little doubt that hunger is made up of various components, and whilst some authorities believe hunger to be essentially reflected in and arising from motility of the empty stomach, others maintain that hunger is not a sensory phenomenon so much as the expression of an inherent urge to remedy the deficiency of nutriment in the body.

There is a close concomitance of fasting motility of the stomach (and intestine) and hunger, but whereas the former is subject to a rhythmic periodicity and is dependent on an inherent automatic mechanism, the latter is a continuous sensation and is closely linked up with metabolic processes.

It seems that the confusion between gastric "hunger" contractions and the hunger sensation is largely due to the different interpretations placed upon the subjective effects produced by gastric motor activity. On the one hand, the conscious sensations due to stomach motility are defined as "hunger pangs" and on the other, the sensations are regarded as visceral manifestations associated with, but not producing, the hunger sensation.

A study of these two factors yields results which tend to support the view that gastric empty contractions and the hunger sensation are separate, but related, phenomena. One is inclined to regard the idea of hunger being the result of motor activity in the alimentary tract, as too superficial an analysis of the problem, and the importance of the biological necessity for food does not seem to receive sufficient consideration on this basis.

Hunger and defensive reflexes are inborn and the ingestion of nourishment is assured in the newly born infant, provided that food is supplied to it, and in this respect the child behaves uncommonly like the decerebrated pigeon. Soon, conditioned reflexes for food are established and as memory develops appetite appears, which in the adult becomes the main factor in feeding in civilised communities.

It cannot be denied that the persistence of hunger after complete excision of the stomach has practically destroyed the theory that hunger arises from empty motility of the stomach and whilst those who tenaciously held to the importance of alimentary activity in producing hunger may now ascribe its origin, in turn, to intestinal factors, the fact remains that central agents must, at present, be admitted to be the most likely influences in initiating the hunger sensation in response to stimuli of various kinds.

The importance of the work of Pavlov in this direction cannot be over-estimated and his investigations, being based on objective physiological findings rather than theoretical comparisons and analogies, form a sure foundation on which to base further experiments with regard to feeding.

The presence of a hunger centre, or centres, is practically established and the effect of chemical and nervous stimulation of the centre have recently been studied from various aspects and indicate the innumerable ways in which its activity may be modified to meet the needs of the organism.

Views are advanced which support the thalamus as being the sub-cortical hunger centre, but if a broader view of hunger is taken which implies, in addition, the efforts of the individual voluntarily to secure and ingest food, then the cortex must contain the more highly complex centres which coordinate these motor reactions.

Carbohydrate and insulin are shown to be of special importance with regard to hunger and hunger motility, although the latter may be inhibited by means of mechanical and chemical stimulation acting locally on the stomach and intestine.

Hunger has been shown to be qualitatively distinct from appetite, the former factor intimating that the alimentary tract of the animal is in a condition capable of dealing with nutriment, and the latter element aiding the initial phase of digestion, the products of which on absorption cause an abeyance of the signal for food.

The association between hunger and satiety can be readily seen, and the latter condition, despite its great variability, induces a condition of nutritive equilibrium in the organism and satisfies its psychic and metabolic requirements.

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